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A RESTUDY OF THE TRACKS OF *PARAMPHIBIUS*

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ABSTRACT

Bradford Willard, 1935, described trails of heteropodous and partially digitate imprints in the Chemung beds of the Upper Devonian near Lanesboro, Pa. Under the impression that the trails were tetrapodous and probably of vertebrate origin, but recognizing certain peculiarities he described a new order of the Amphibia, the Ichthyopoda; a new genus, *Paramphibius;* and two new species, *Paramphibius didactylus* and *Paramphibius tridactylus*. New material from the type locality indicates that *Paramphibius* was a merostomè, probably closely related to the Devonian xiphosuran *Protolimulus*. This conclusion is supported by the paleoichnology of the Xiphosura, by evidence obtained from the study of the modern king crab, *Limulus polyphemus*, and by considerable environmental evidence. Up to the present time there seems to be no evidence of amphibians in the Devonian system of North America.

PART I: ICHNOLOGY

Great numbers of peculiar tracks and trails in the Kingsley shale of the Chemung stage of the Upper Devonian near Lanesboro, Pa., have elicited considerable controversy among those who have examined them. Oral interpretations have ranged all the way from seaweed ("fucoid") impressions through tracks of various sorts, including most kinds of arthropods, and finally to the vertebrates. The last interpretation has been developed rather extensively by Dr. Bradford Willard (1935) in a paper that first attracted my attention to the problem.

Willard described these trails under the name *Paramphibius* on the basis of a rather small collection. He came to the conclusion that the trail maker was a vertebrate, principally because of peculiar pentadactylous footlike impressions that recall modern newts and salamanders. These impressions alternate in series with braces of biramous impressions such as might be made by the split fin rays of certain existing fishes. He thought of *Paramphibius* as occupying a systematic position somewhere between the Crossopterygian fish (with certain teleost characters) and the most primitive Stegocephalian amphibians. For this purely hypothetical group he proposed and described the amphibian order Ichthyopoda. He supposed that the ichthyopods walked in much the same manner as certain of our present-day land-traveling teleosts. It would of course be difficult to reconcile[1] an order of this construction with the longstanding view of comparative anatomists and paleontologists that the anterior and posterior paired appendages of tetra-

[1] One is reminded in this connection of the words of encouragement given by Huxley to the originator of the Echinoderm theory of vertebrate origin which rather startled zoologists at the time: "Go forth and prosper; there is nothing so good for science as one of those earth-quake hypotheses which make us suddenly realize that the solidest-looking structures may collapse."

pods are homologous. All other structural characters inferred for the track maker rested on this interpretation. He suggested that the environment of *Paramphibius* was probably fresh water and continental, and assumed that the animal moved in a striding manner when under water and by hitching when on land—a reversal of the usual picture of the origin of the vertebrate manner of walking.

This paper will develop the thesis that *Paramphibius* was not a vertebrate but an ancestral king crab. Evidence is at hand to indicate that the track maker was, in descending order, an arthropod, arachnid, merostome, xiphosuran, and limuloid organism that was closely related to, if not generically synonymous with, *Protolimulus* of the Upper Devonian. In logical arrangement the steps by which this conclusion has been reached are as follows:

Arthropod: An abundance of material from the type locality establishes beyond question that *Paramphibius* was twelve-footed. From the regularity and uniformity of the pedal impressions and the impressions of what are clearly chitin-bound articulations, the nature of the jointed, segmented legs is established. Appendages of this number and construction are restricted to the Arthropoda. It will also be shown that the legs were terminated by chelae, which are likewise exclusively arthropodous. A comparison of the tracks of *Paramphibius* with other known arthropod tracks, fossil and recent, seems to clinch this argument.

Arachnid: There is good evidence that *Paramphibius* had a more or less rigid chitin-clad body made up of three pieces—head piece, mesial piece, and rigid tail—which are analogous, if not homologous, to the cephalothorax, buckler, and telson of xiphosurous arachnids. There is also evidence of gill books.

Merostome: Inasmuch as *Paramphibius* was an aquatic arachnid, as will be brought out in the second part of this paper, it must have been a merostome. In addition, the six pairs of walking legs arranged presumably about the mouth and serving basally as coxal organs of manducation, and the presence of chelae on the first pair of legs (chelicerae) all bespeak the Merostomata.

Xiphosuran: According to Woodward (1867), the limuloids and the eurypterids (tribe Poecilopoda of McCoy, 1854) are characterized by their didactylous ambulatory thoracic feet. Certainly this is a character of high importance, in the Xiphosura at any rate, which the tracks exhibit. Of particular structural and historical significance in determining the xiphosuran origin of the tracks is the evidence of foliate "pushers" on the posterior pair of legs.

Limuloid: On the basis of a pair of pushers, rounded anterior digging-margin of the head, and a variety of ventral impressions, including those of the holding border and abdominal or buckler spines, and especially from a detailed comparison with the trails made by modern immature limuli and fossil limuloids from the Devonian to the Recent, it seems cer-

tain that *Paramphibius* was closely related to if not even identical with *Protolimulus*, and therefore probably in the ancestral line of modern horseshoe crabs.

GENERAL DESCRIPTION

The trails[2] of *Paramphibius* consist of bilateral footprints of two kinds, which occur in the most perfect trails in the proportion of five to one. Commonly, however, the front pair of appendages leaves no impression, thus making the common proportion four to one. The more numerous impressions, here referred to as simple tracks, are characterized by terminal chelation (fig. 1, *a*). Closer observation shows that they occur in groups of five pairs, of which the first stood closest together, succeeding pairs being progressively farther apart (figs. 1, *b* and 5, *1-5*). The second kind of tracks consists of a single pair. These are digitate (figs. 1, *c* and 3, *d*) and are usually superimposed upon the simple tracks at about the impression of the fourth pair of feet (figs. 1, *d* and 5, *6*). These hindmost "digitate" tracks are characterized by five anterior radiating blade imprints (fig. 1, *c*, *bl*) and a disjunct posteriorly directed bar impression (fig. 1, *ch*,) which terminates distally in the impression of a pair of unequal movable spines, (fig. 1, *c sp*). The hind tracks are so similar to the impressions made by the whorled pushing apparatus on the sixth pair of appendages of *Limulus* that they are best described as "pusher-prints" (fig. 3, *c-d*). All the "pusher-prints" of *Paramphibius* are more deeply impressed than the simple tracks and seem to have been made by the principal organs of locomotion when walking.

Very few trails of *Paramphibius* show the impressions of all five pairs of simple feet. Usually the first pair left no impression. The number of impressions left by the remaining four pairs of simple feet varies considerably. Differential pressure on the various feet, or actual omission of the impressions of certain feet during some kinds of locomotion are in evidence (e.g., pl. 2 fig. 5; pl. 3, fig. 2; pl. 6, fig. 3). Many of the weaker impressions were lost in the field because the paper-thin laminae of the rock are apt to split off from the surface bearing the tracks. This condition is shown on plate 9, figure 1, and plate 6, figure 4. It would seem inadvisable therefore to differentiate species of *Paramphibius* on the basis of the number of simple tracks occurring in a trail. The type material of *Paramphibius* showed at most only three pairs of simple tracks and much of the material recorded the imprints of only two pairs. The two species *P. didactylus* and *P. tridactylus* were defined chiefly on this distinction in the trails. It seems best tentatively to consider *P. tridactylus* a synonym by page priority of *P. didactylus*.

The trails illustrated on the plates

[2] The terms "trail" and "track" are used in this paper in the sense advocated by A. W. Packard, *Am. Acad. Sci. and Arts, Proc.*, vol. 36, no. 4, p. 63–71, 1900, wherein he proposed that the term "trail" be restricted to a series of footprints made by an individual, and the term "track" restricted to the individual footprint.

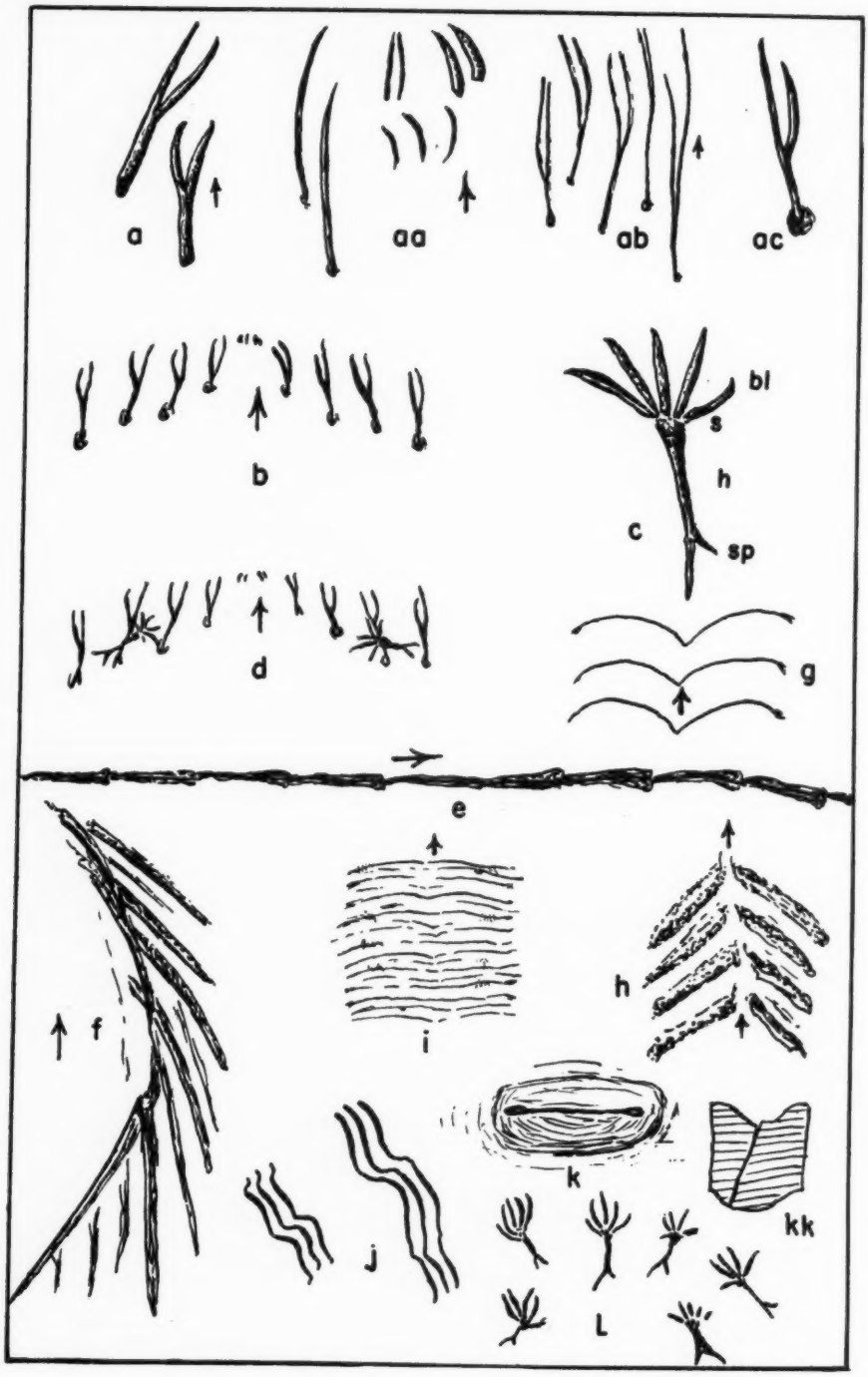

FIG. 1.—(*See opposite page for explanation*)

are chiefly natural size. Specimens in the writer's collection range in width or "straddle" (Matthew, 1909) from 5 mm. or less to more than 40 mm. Many of the trails have been followed for as much as 4 feet where they were terminated only by the face of the quarry. The upper trail zone at Lanesboro is a veritable mat of trails, most of which run in the same general direction, which is thought to be shoreward (Part II, this paper). This is particularly true for the larger trails (adult?), which show a very striking fixity of purpose and directness of route. Many of the trails attributed to immature specimens are sigmoidal or even circuitous but do show the directional tendency of the adult trails. Several of the larger trails seem to have been willfully superimposed upon each other, so well do they coincide. From the absence of resting impressions and also of carcasses it seems clear that the Lanesboro record is that of migrations rather than normal living. In the Lanesboro quarry the trails occur at two or more horizons, which are separated by a few inches of barren shale. From this recurrence of the trails a periodicity of migration is suggested.

Certain clots of mud, such as shown by figure 1 on plate 3, terminate some of the trails of *Paramphibius*, and others of the same sort occur in the midst of the trails (e.g., pl. 2, fig. 1), thus obscuring the footprints for a short distance. This may represent places where the organism sank in vertically for protection or in seeking a morsel of food. It seems quite clear, however, that *Paramphibius* was chiefly engaged in walking on the surface and not in burrowing when the Lanesboro tracks were made.

The trails carry certain additional impressions, which are of considerable importance in interpreting *Paramphibius*. Most common of these is a median groove or furrow (fig. 1, *e* and fig. 5, *tg*), which commonly thins and widens as though made by a rigid tail that was occasionally raised and lowered. Not everywhere is this swelling and diminishing of the median groove obvious, which suggests an organism contentedly dragging its tail. In a few places, and this not too certainly, it appears that the tail may have been inserted into the mud with a backward push; in many places a record is preserved, as shown on plate 8, figure 3, of a furious lash-

FIG. 1.—Certain details of the *Paramphibius* trails: *a*, a simple track illustrating the terminal chelation; *aa*, simple tracks made by chelate feet used in a scratching manner; *ab*, long Y-shaped scratches made by simple feet used as in *aa; ac*, simple tracks with proximal mound of mud, which is attributed to filling of an articulatory surface; *b*, a brace of simple tracks showing usual position of tracks during ordinary forward walking; *c*, a pusher track with parts named (*bl*, blades; *h*, heel; *s*, sole; *sp*, spines); *d*, showing usual position of pusher tracks in reference to a brace of simple tracks; *e*, a series of tail grooves showing anterior bluntness of the impressions; *f*, impressions made by a lashing tail; *g*, series of holding-border or "terminally inverted printers braces" impressions; *h*, mesially interrupted "chevrons"; *i*, markings attributed to pulsating gill books; *j*, lateral drag marks attributed to abdominal stylets; *k*, "dumb-bell" incisions associated with the tracks; *kk*, vertical section through "dumb-bell" incision showing deformation of the strata and slight "faulting" that always accompanies the incisions; *l*, several pusher tracks showing some of the commoner variations observed. Arrows indicate direction of movement.

ing of the tail when the animal was apparently stuck in the mud. Most of such markings are anteriorly truncate, posteriorly attenuated, and uniformly of the same size for a given trail (fig. 1, *e*). The suggestion of a rigid ensiform telson is almost inescapable.

Some less common markings are very clearly preserved in the trails. Most striking of these is the serial impression of a transverse carina having the general shape of a printers' brace with the wings reversed (fig. 1, *g*, and pl. 9). The terminations of the wings of most of the impressions are very slightly bifid, as shown by figure 1, *f*, and plate 9, figures 3, 4. This is almost identical in shape with the inner edge of the underside of the cephalothorax of *Limulus*, i.e., the posterior or "holding border" of the expanded hypostomal plate, (fig. 2, *Hb*). In *Limulus* the "holding border" is not apparently terminally delicately bifid as was the imprinted structure in *Paramphibius*. Impressions of this border in *Limulus* are shown on plate 12, figures 2, 6. The serial impression of another edge, which was broadly convex anteriorly, may have been made by the front margin of the head, and suggests the "digging ridge" of *Limulus* (figs. 2, *Ac*, and 5, *c*). This latter trace is in most places very indistinctly preserved (e.g., pl. 4, fig. 2).

In many of the trails a more or less continuous groove forms the outside border. Continuous grooves of the sort seen on plate 9, figure 7, and plate 11, figure 4, are most common. In some trails these border grooves are more or less "chatter marks" which are made of regularly spaced synchronous gouges (fig. 5, *Sg*). The gouges seem to have a constant relation to the series of footprints. They are respectively similar to two types of grooves made by the genal spines of *Limulus:* first, when walking with head anteriorly uplifted, spines continuously dragging; and, second, when lifting the head anteriorly highest only when pushing forward. The second type is shown by figure 5, *Sg*. Both types are shown on plate 12, figure 1. A less common and usually indistinct type of outside grooves occurs a little farther from the median line than those compared with genal-spine grooves. They are furrowlike, being usually rather sharply incised on the outside edge and rather indistinct on the inside (fig. 5, *Srg*). These grooves are not unlike those made by *Limulus* when using the outer edges of its cephalothorax like sleigh runners (e.g., pl. 13, fig. 8). Both types of parallel grooves may occur in the same trail, but they seem to be mutually exclusive. They are not both present at the same place on a trail, as the diagrammatic representation in figure 5 might lead one to believe.

In some trails a serial arrangement of broad chevronlike markings, which are mesially interrupted, has been observed. These markings seem to be of two kinds. One kind is restricted to the area adjacent to the median line (pl. 9, fig. 1) and is in many places additionally obscured by the mesial drag mark. These suggest the impressions of the basal

joints of the gnathopods of a merostome (fig. 1, *h*). The second kind of chevronlike serial impression is in most places very indistinct and is frequently found where tracks are only very incomplete (fig. 1, *i*). They suggest the ripple marks made on the bottom sediment by the pulsating gill books of a partially swimming *Limulus*, such as can be seen in any salt-water aquarium, and were first described by Dawson (1862).

With the trails, both in series and independently in the same layers, are very delicate bilaterally symmetrical bracelike markings, which are so faint on our material that it is very difficult to represent them. The strongest marks of this type are shown in the vertical series on plate 9, figure 5. They are evidently contact marks made by the edge of a very fragile organ, and may be tangential opercular imprints such as are made by *Limulus* when swimming very close to the bottom. The commonest other trail mark associated with these markings is an occasional short drag groove, evidently made by the end of the same organ responsible for the median furrow of the trails. Lloyd (in Owen, 1873, quoted by Woodward (1878), p. 190) has described the rather common mode of progression in *Limulus* whereby the swimming animal occasionally touches bottom with its tail to keep it off the sea floor. The parallelism is intriguing. Such drag marks are shown on plate 11, figure 7.

In some of the circuitous trails, the animals careened on curves to a considerable degree. In some places the impressions of all appendages on the outside of the curve are omitted, but usually the pusher imprint is recorded. In several places the animals careened so far that impressions of lateral posterior spines (stylets) were left on the inside of curves (fig. 1, *j*, and pl. 9, figs. 2, 5). The position of the grooves made by these spines indicates a posteriorly tapering body to which the spines were attached. The grooves left by the buckler spines (stylets) of *Limulus* (pl. 13, fig. 6) are almost identical with those in the *Paramphibius* trails.

Certain incisions having a dumbbell-shaped cross section occur abundantly with the trails of *Paramphibius* (pl. 11, figs. 1, 3; pl. 4, fig. 6) and may represent impressions of its ovipositor (fig. 1, *k*). They are more fully discussed under the heading of "Problematica," in Part II of this paper.

The simple tracks of *Paramphibius* are about four times as abundant as the pusher impressions. Some characteristic simple track impressions are shown in figure 1, *b*, and on the plates of photographs. It is clear from the drawings and photographs that the impressions were definitely chelicerous, i.e., the longer side of the simple impression is in a fixed position relative to the shorter and opposable side. All the simple prints show a definite hinge action between these two parts of the track (pl. 5, fig. 1) except in the rather rare cases when only the ends of the claws were dug into the mud to form short single (pl. 10, fig. 5) or parallel scratches

(fig. 1, *aa*, pl. 8, fig. 5) or more or less elongate Y-shaped markings made by claws that were opened to a varying degree when the scratch was begun, but were closed before the scratch was completed (fig. 1, *ab*; pl. 7, figs. 6–8). There is considerable variation in this latter type of scratch. It is important when interpreting the tracks to differentiate clearly between impressions of appendages and scratches and abrasions made by appendages during locomotion. The size of the impressions of the simple feet increases posteriorly, but in each case the impression of the chela is approximately two-fifths as long as the entire simple impression. The two halves of the chela usually terminate subequally, but in observed cases of inequality the movable bar has ended before the fixed portion. In the impressions, the bar always opens backward, as would be expected; and, as is clearly shown in figure 1, *a*, and plate 1, figure 1, the angle formed by the bar and the fixed portion is highly variable (pl. 1, fig. 2). In the trails of the largest individuals this angle is seldom over 30°, but in smaller trails there seems to have been greater flexibility of the chelae. A few well-preserved tracks seem to record the impressions of a definite arthropodous claw joint (pl. 5, figs. 1, 2; pl. 6, fig. 1). In the mud at the proximal end of several simple tracks there is a distinct cuplike depression or small elevation that suggests the vertical impression of the proximal part or segment of the simple leg (fig. 1, *ac*; pl. 8, fig. 4; pl. 1, fig. 3; pl. 4, fig. 1). The simple feet are usually directed anterolaterally, but terrain and other factors frequently modified this placement, as the photographs show. In a few trails, the V-shaped, converging scratch or double-dot impressions of the first pair of appendages are recorded near the median line (fig. 1, *b*, and pl. 1, fig. 1; pl. 2, fig. 3). The complete impression of the simple feet on one side of the body, exclusive of the first foot, are here referred to as a "brace" (brackets in fig. 5).

The sixth pair of tracks (pusher impressions) were the chief basis for the original interpretation of *Paramphibius* as a vertebrate. They are strikingly like some of the footprints of the early stegocephs or even of modern newts and salamanders, especially when not clearly impressed. How else to explain five toes and a heel? As Willard has shown, these pentadactylous imprints are usually directed anteromesially in a "pigeon-toed" manner (pl. 4, fig. 1). This trend is nearly at right angles to the normal anterolateral trend of the simple tracks (fig. 1, *d*, and fig. 5). In straight-ahead walking the pushers were usually impressed as a surcharge upon the imprints of the fourth pair of simple feet and intersected them near their middle.

There are three parts to each pusher imprint: 1, an anterior fanlike impression made by five digitlike structures, which radiate disjunctly from, 2, the end of a bar impression, which is swollen slightly at each end. This was the original "heel" of *Paramphibius*. It is terminated, 3, by

the imprints of two mutually movable unequal spines. The pusher seems to have been consistently five-bladed. The blades were lanceolate and more or less rigid. They were arcuate in cross section and were impressed in the mud with the concave side down. The blades were of varying length, but usually of similar pattern and proportion, the longest usually being the second from the outside (fig. 1, *c*; pl. 1, figs. 4–6; pl. 2, figs. 4, 6). As shown by the drawings and photographs, the impressions indicate that all the blades were slightly curved on their longitudinal axes toward the median line of the animal. There seems to be a direct ratio between the degree of expansion of the blades in the pusher impressions and the amount of impressure of the "heel" bar in the mud. The angles formed with each other by the blade impressions is highly variable as the drawings show (fig. 1, *l*). The impressions indicate clearly the pushing function of the sixth pair of legs. The blades seem to have been inserted in at least a partly expanded state, points first in the mud, then to have spread farther apart as the weight of the animal came to rest on them. Usually the whole pushing structure seems to have collapsed into more or less of a "flat foot" at this juncture. In many tracks the blades were so oriented that the sharp outer edges cut the mud and side-slipped downward slightly until caught by the lower concavity of each blade. This creates an illusion of frailty in many of the *Paramphibius* pusher tracks but in reality only the narrow incisions of the blades show up (fig. 1, *l*; pl. 7, figs, 2, 7). In other tracks the blades seem to have been pressed down very flatly in the mud (fig. 1, *l*; pl. 2, figs. 4, 6).

Behind the impressions of the blades there is usually a tiny elevation of the mud, as though it had been crowded into a joint (fig. 1, *c s*), which was originally described as the sole of the amphibian foot. The heel bar or handle to the pusher fan (fig. 1, *c h*) is about one-third longer than the longest pusher blade of the track and is nearly equal to the chelate impression made by the fifth pair of simple legs. The swollen extremities of the bar give it an attenuated dumbbell shape. Usually the posterior end of the bar is more deeply impressed than the front end. It also frequently appears that the bar was pushed backward a little after being first imprinted. This is one phase of the so-called collapse of the pusher into a "flat-footed" structure. The terminal spines at the end of the bar are always opened at an angle, the degree of which varies considerably in different tracks. Both spines open outward from alignment with the bar, but the outer spine is always opened farthest from alignment (fig. 1, c *sp*; pl. 2, fig. 4). That the spines were mutually movable is abundantly demonstrated by the plates.

A COMPARISON OF *PARAMPHIBIUS* WITH *LIMULUS*

The basis for the present thesis lies in the ichnological data already dis-

cussed and illustrated. It is now proposed to make a structural and functional comparison of *Paramphibius* and *Limulus*, with the object of interpreting the tracks and trails. I propose, first, to discuss briefly the appendages of *Limulus*, with especial attention to those parts that leave an impression in the walking trail, and compare those impressions with the elements in the trails of *Paramphibius*. From the structural comparison, with the assistance of experiments with living crabs, I propose, second, to compare the locomotion of *Limulus* and *Paramphibius* and also to draw certain other functional conclusions. The terminology used for the organs of *Limulus* is essentially that of Owen (1873) and Woodward (1865–1878).

The cephalothoracic appendages of Limulus.—The ventral anatomy of *Limulus* is shown on the right side of figure 2. The cephalothoracic appendages are principally six pairs of gnathous circumoral appendages, which serve as organs both of locomotion and manducation.

1. Anterior to the mouth and not partaking of the gnathous function of the other appendages are a pair of palpiform *antennules* (fig. 2, I). These are chelate like all the other circumoral appendages of *Limulus* and are probably the homologues of the chelicerae of the eurypterids. They are seldom used in locomotion, and apparently only by accident ever leave their impressions in the trails of *Limulus*.

2. Behind the antennules are five pairs of chelate "jaw-legs" or *gnathopods*, which are essentially similar in structure and function. The nomenclature used for these was based on the assumption that they are homologous to similarly located organs in the Crustacea. The first pair of gnathopods are known as *antennae* (fig. 2, II).

3, 4, 5. There follow in order three pairs of gnathopods of similar structure but of increasing length posteriorly, the *mandibles* (fig. 2, III) and two pairs of *maxillae* (fig. 2, IV, V). The mandibles and the maxillae together are known as the *endognaths* (fig. 2, En).

6. The hind pair of gnathopods are the *maxillipeds* or *ectognaths*, which are commonly known as pushers from their function (fig. 2, VI). The penultimate segment of the maxilliped bears distally a whorl of four (sometimes five?) leaflike, movable blades, which collectively constitute the main pushing organ (fig. 2, *fl*).

The terminology of the segments of the gnathopods of *Limulus* is likewise borrowed from entomology and carcinology. The maxillipeds are made up of seven segments and the anterior five pairs of appendages of six segments. These segments from the base outward are known as: 1. *coxa*, or "haunch" (fig. 2, *c*). When serving the function of jaws the coxae are known as *coxagnaths;* when simple, as *coxapods*. Then follow outward, 2, the *basos* or basis (fig. 2, *b*); 3, *meros*, or merion (fig. 2, *m*); 4, *carpus*, or cnemon (fig. 2); *cp*5, *propodos*, or propes (fig. 2, *p*); and terminally, 6, the *dactylus* (fig. 2, *d*). In the maxillipeds a seventh segment,

the *unguis* (fig. 2, *un*), terminates the leg. In the simple legs the propodos and dactylus make a chela (fig. 2, *ch*). In the maxillipeds the unguis and a movable spine (fig. 2, *ms*) make a pseudochela (fig. 2, *fc*), both halves of which are movable. In the simple legs the segments distad of the coxa make up the palpus as that term is commonly used. An alternative usage is illustrated by Owen (1873) as quoted by Woodward (1878, p. 190): "In the cephaletral limbs the haunch joint (coxal) is of great-transverse extent, and besides affording insertion of the apodemal muscles which forcibly work the carding-plate (of the coxa) or palpus, pl. 34, fig. 2–5, gives origin . . ." The pusherwhorl (fig. 2, *fl*) of the maxilliped is attached to the distal end of the propodos.

The appendages of Paramphibius.—As a comparison of figure 1 and the plates will show, every structure known in the trails of *Paramphibius* is closely duplicated in the trails and tracks of modern *Limulus*. It is assumed that tracks so closely similar in detail must have been made by closely similar organs. In *Paramphibius* there have been found braces of simple footprints that indicate five pairs of simple chelate feet, upon which the impressions of the hind pair of pushing feet were superimposed. The hind pair of pushing feet bore five pusher blades in *Paramphibius* rather than four as in most modern limuli. (Compare pl. 2, figs. 4, 6 with pl. 12, fig. 3.) But here the difference in locomotor organs apparently ceases. Figure 2 shows on the right side the chief appendages of *Limulus* and the nomenclature of the segments of the legs. On the left side are shown by solid lines the *Limulus* structures whose homologues are inferred for *Paramphibius*. The chief bases for drawing these homologues have been shown in figure 1 and the plates of photographs.

The walking legs of *Paramphibius* were definitely chelate, as the tracks so clearly show (fig. 1, *a*, *b*, and plates). The impression of the chelate segment is almost identical with that of the homologous leg of *Limulus*, when the end segment in the latter is forced down flat into the mud to simulate the usual position in *Paramphibius* (pl. 13, fig. 5). The longer part of the terminal segment of *Paramphibius* was probably the penultimate segment, or propodos, and the movable bar the true terminal segment or dactylite, as in *Limulus*. It is interesting to see how very ancient this chelate specialization is among the Xiphosura Limulida (see Størmer, 1934, for summary of classification).

It would also appear that in *Paramphibius* the "antennules and antennae" were already as far removed from functional antennae and antennules in the crustacean sense as in modern *Limulus*. Terminally the antennae were identical with the other walking or simple legs, except for smaller size. The antennules were apparently usually carried in an upfolded or dangling position as in *Limulus* and only by accident left their peculiar scratches or impression in the mud. The endognaths in *Param-*

phibius were principally food-grasping organs apparently as in *Limulus*, and served largely as resting organs in the process of locomotion, although on occasion they may also have been used to aid in pulling the

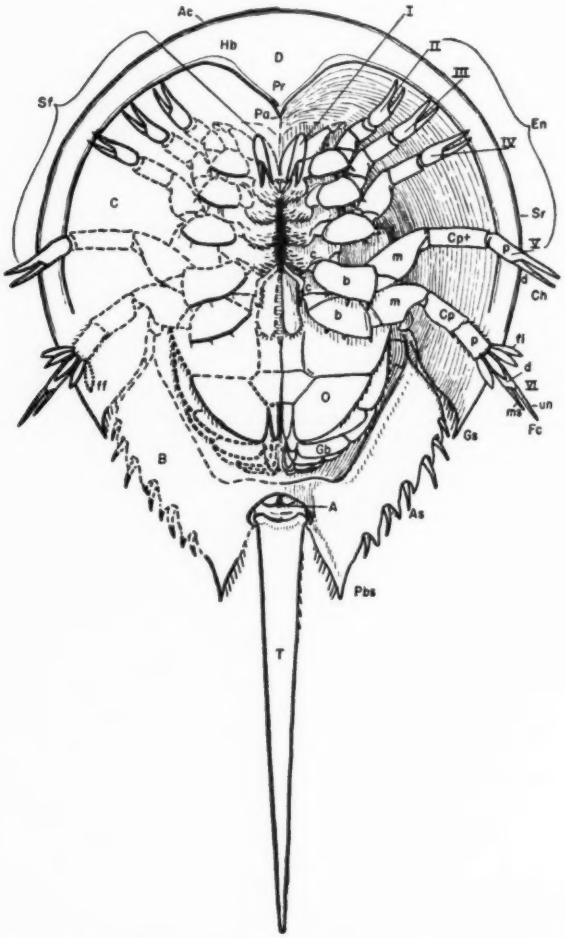

FIG. 2.—Ventral view of an immature specimen of *Limulus polyphemus*, from Woods Hole, Mass.; right side shows chief external anatomical characters of *Limulus* that leave an impression in the trails; left side shows by solid lines those parts of *Limulus* that seem to have homologues in *Paramphibius* as inferred from the tracks and trails. Symbols: A, anus; Ac, anterior doublure-carina or burrowing-carina; As, abdominal or lateral buckler spines; Ch, chelae; D, doublure; En, endognaths; Gb, gill books; Gs, genal spine; Hb, holding border or carina; O, operculum; Pa, prostomial angle; Pbs, posterior buckler spine; Pr, prostomial region; Sf, simple feet of *Paramphibius;* Sr, "sleigh-runner" arc of cephalothorax; I, antennule or chelicera; II, antenna; III, mandible; IV, anterior maxilla; V, posterior maxilla (III, IV, V, endognaths); b, basos; c, coxa or coxognath; cp, carpus (cp+ may be cp plus p); d, dactylus; m, meros; p, propodos; b–d or un, palpus; ch, chelae; VI, maxilliped or ectognath; fl, pusher; ff, fifth pusher blade in *Paramphibius;* ms, maxillipedal spine; fc, false chela; u, unguis. Drawing by A. S. Caster.

organism along the bottom (fig. 1, *aa*, *ab*, and pl. 13). In walking the entire terminal segment was laid flat in the mud, and at nearly a right angle to the carpus, the end of which is sometimes impressed (fig. 1, *ac*). This condition is found in modern *Limulus* only in the very young forms, or when pressure is exerted which forces the animal unnaturally to bend the joint between the carpus and propodos (pl. 12, fig. 3).

The maxillipeds or pushing legs of *Paramphibius* were functionally very similar to the homologous structure in modern *Limulus* and other Limulida. They comprised a whorl of five instead of four lanceolate blades, which were attached to the anteroventral side of the propodos and were apparently expanded by muscles, leverage, or both when the dactylus was underflexed to form the so-called "heel" impression. The degree of expansion of the blades of the pusher and the angle made with the underbent dactylus seemed to depend directly on the energy expanded by *Paramphibius* in pushing ahead, which is precisely the condition observed in the locomotion of immature limuli (fig. 3).

Figure 3 represents camera-lucida drawings of the pusher and maxilliped track of *Limulus polyphemus* at various ontogenetic stages and a reconstruction of the distal end of the maxilliped of *Paramphibius* based on the Lanesboro tracks. The principal reason for selecting immature specimens of *Limulus* for experiments in the laboratory (outlined below) is obvious from this diagram In the earlier stages of development *Limulus* leaves walking trails very much like those left by *Paramphibius*, and subsequent changes in the trails are principally due to adult modification, chiefly chitonization, of the pushing apparatus in the manner shown here. After *Limulus* is more than 1½ inches long the pusher blades are gradually strengthened, their pushing function is improved, and the maxilliped impressions are no longer pes-like, as they were in immaturity and in *Paramphibius*. From the tracks it seems that in *Paramphibius* the pair of terminal movable spines on the maxilliped were amazingly similar to those in *Limulus*. They seem to have had little use in *Paramphibius*, and are commonly worn off in old specimens of modern king crabs.

The abdominal appendages of *Paramphibius*, insofar as the tracks intimate, were booklike modifications in general like those of *Limulus* and the Limulida. The indistinct markings made in the trails of immature limuli by the gill books and operculum are duplicated faithfully in the trails of *Paramphibius* (fig 1, i).

Limulus trails and locomotion.— When it became clear that the prosomal appendages of *Limulus* are capable of making tracks very similar to those made by *Paramphibius*, a search for information on the trails made by *Limulus* was undertaken, so that the comparisons could be carried farther. There is considerable literature (Dawson, 1862, 1873; Owen, 1873; Woodward, 1865–1878;

Lockwood, 1870; Packard, 1870–1880; Arnold, 1929; Abel, O., 1934) on the habits of *Limulus* in nature and in aquaria, but almost universally the accounts deal with mature crabs. It became clear in examining the maxillipeds of *Limulus* and the tracks made at various stages of development (fig. 3) that the closest similarity occurred between the tracks made by early post-embryonic crabs and *Paramphibius*. It is the type of parallelism one would expect in a phylogenetic line if the biogenetic law were applied.

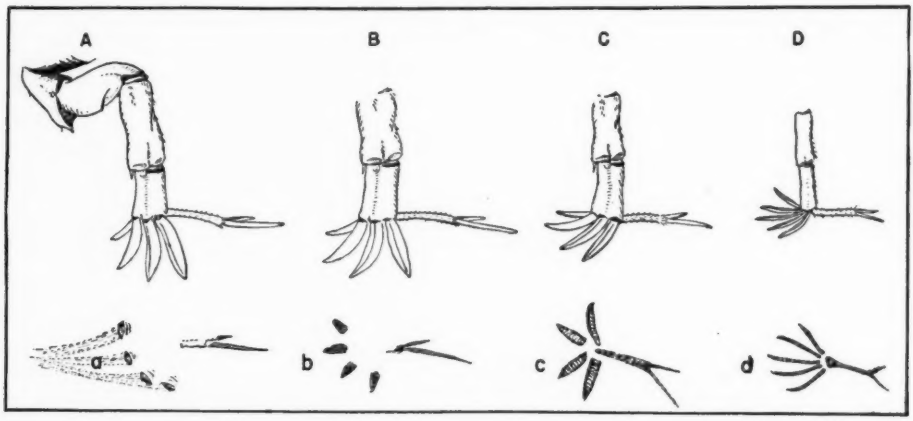

FIG. 3.—Camera-lucida drawings of the fully distended maxillipedal pushers of *Limulus polyphemus* at three stages in ontogeny, and the hypothetical adult pusher of *Paramphibius didactylus* as judged from the tracks in the Kingsley shale near Lanesboro, Pa. Below the drawings of the pushers are camera-lucida sketches of the tracks made in mud by the respective maxillipeds. A, subimago stage of *Limulus polyphemus;* B, nymph stage; C, early post-embryonic stage; D, terminal joints of the maxillipedite of adult *Paramphibius* as inferred from the tracks. Lower-case letters represent tracks made by flabella of corresponding capital letter. The dotted lines in track *a* represent the drag of the pusher blades in mud or sand as they were removed to make the next track impression.

Limulus has three methods of locomotion, which anyone can observe in a salt-water aquarium. It occasionally swims by use of the prosomal appendages, folding of the buckler against the cephalothorax, waving of the operculum and gill books, and sculling operation of the telson. Apparently any combination of these organs is possible and a form of swimming results. Only when the organism swims close to the bottom does this operation leave a trail, which consists of ripple-marks made by the fanning of the gill books, occasional scratches made by the chelicerate feet, an occasional gouge or furrow made as the telson is lowered to push the organism off the floor, and an occasional pusher impression. This operation was described by Lloyd in Owen (1873) and Woodward (1878, p. 190) and by Packard (1900). The trails of *Paramphibius* shown on plate 11, figure 7, and plate 7, figure 7, are thought to have been made in a similar manner.

In an aquarium that has very little sand or mud on the bottom, *Limulus* can be seen walking over the surface or ploughing as deeply as possible in the sediment on the floor. In its normal environment of moderately deep water, 2 to 6 fathoms (Lockwood, 1870, pp. 254–270), it apparently seldom appears on the surface of the bottom mud. Quoting Lockwood, 1870:

> It is emphatically a burrowing animal, living literally in the mud, into which it scoops or gouges its way with great facility by means of the anterior edge of its enormous cephalic shield. In the burrowing operation the forward edge of the anterior shield is pressed downwards and shoved forwards, the two shields being inflected, and the sharp point of the tail presenting the fulcrum as it pierces the mud, while underneath the feet are incessantly active scratching up and pushing out the earth on both sides. There is a singular economy of force in this excavating action, for the alternate doubling up or inflecting, and straightening out of the two carapaces with the pushing-purchase exerted by the tail-spine, accomplish both digging and subterranean progression. Hence the King Crab is worthy to be called the "Marine Mole."

Lockwood and others have pointed out that *Limulus* apparently never seeks the shallow water save for the purpose of reproduction, when the adult crabs literally swarm into the shallow waters and tidal pools in late May and June, walking singly and in pairs or strings (Owen, 1873; Arnold, 1929). This seems to be the only occasion when the crabs walk extensively on the floor of the sea and make tracks such as would be useful in this study. The process of burrowing naturally obliterates all track detail. The trails of several adult crabs that were left by the tide on the sandy shore of Long Island during the mating season are shown in figure 4. Such trails have been described in detail by Dawson (1862).

Through the courtesy of the Marine Biological Supply House of Woods Hole, Mass., several specimens of immature *Limulus* ranging in length from a little less than 45 mm. to 75 mm. were procured in a salt-water aquarium and maintained in the laboratory for several months during 1936–37. The aquarium was furnished with a floor of washed sand about 2 inches deep at first. Immediately the crabs burrowed beneath the surface and were seen only when dug out. When the floor covering was reduced to half an inch or so they were content to plough through this, or even walk-swim over the surface, leaving a few ripples, chelate scratched, and an occasional tail groove as a track record of which no successful photographs were taken, but which was very similar in detail to the *Paramphibius* trails shown on plate 4, figure 3, and plate 7, figure 7. By feeding the crabs fragments of clams or oysters, their activity was materially reduced, and it was found that they would readily kill themselves by overeating!

Experiments were then tried to duplicate with hungry crabs the conditions under which mating trails are made naturally along the seashore in May and June. Pans were filled with glacial lake clay, dampened with salt water to varying degrees of plasticity and the young crabs placed on the clay. When hungry they would im-

mediately start walking and pushing over the clay. They showed no desire to burrow unless the clay was very wet or under half an inch or so of water. But the application of even a few drops of water to the carapace of a walking crab was often sufficient to cause it to start ploughing into the mud, or to make an attempt to hide itself by sinking in vertically. It was found that trails and tracks most closely resembling those made by *Paramphibius* were made by wet crabs (and they retain their ventral wetness from water in the gill books for considerable time) on clay of about the consistency of finishing plaster when applied. The details of these trails were preserved by making plaster of paris casts as soon as the pan of trails was completed. The photographs shown on plates 12 and 13 are of the plaster casts made before the mud had dried. By the addition of considerable mica to the clay it was found that mud-cracking upon drying was materially reduced, and some of the trails could be photographed directly.

The activity of *Limulus* on the sea floor is divisible into walking habits and burrowing habits. There are two types of burrowing habits: common forward undersurface grubbing or ploughing, which is apparently the chief activity of *Limulus* in its usual environment, and protective vertical excavation by which it hastily protects itself if accidentally exposed while burrowing or if startled while walking.

In all forms of locomotion, the most fundamental movements consist of folding the cephalothorax and buckler toward each other ventrally. The varying movements of the appendages abet this movement (Owen, 1873). In walking on the surface as shown in figure 5, which demonstrates locomotion for *Paramphibius*, the endognaths serve principally as resting organs, which hold up the prosoma while the flexed maxillipeds and buckler are uplifted and the former placed. The maxillipeds are then straightened, the prosoma being uplifted anteriorly and the endognaths freed from the surface; as the maxillipeds are straightened, the blades catch the mud and the whole organism moves ahead. The telson may assist in the pushing action if friction or hurry warrants. In very young crabs the endognaths rest essentially vertically in the mud to form two tiny pricks where the chelae enter. These are extended into scratches forward when they are removed and the prosoma is pushed ahead by the straightening of the maxillipeds and prodding of the telson where necessary. Seldom are the endognath joints between the carpus and propodos bent sufficiently to allow the chelae to lie flat in the mud as they did in *Paramphibius*. See plate 13, figure 1, for comparison.

Usually only the posterior two or occasionally three pairs of simple feet are recorded in the walking trail. Almost never are the antennules imprinted unless the animal becomes bogged down. The simple feet are usually directed anterolaterally, and their impressions leave broad, anteriorly directed chevrons of pricks

and scratches. Their direction may vary, however, owing to currents, obstructions, or for no obvious reason, much in the same manner as a dog may run forward with its body oriented to the right or left. The adult crabs tend more and more to push themselves along on the sleigh-runner-like ventral lateral edges of the cephalothorax (fig. 2, Sr) rather than lift themselves on the ends of their simple legs (Dawson, 1878).

This activity results in a trail of the sort shown on plate 13, figure 8, in which the most prominent tracks are those of the maxillipeds, the median drag mark of the telson, and lateral grooves made by either the genal spines or ventral lateral arc of the prosoma, or both. Variations in the walking trails depend on the resistance of the mud, circuitousness of the trail, and obstacles in the path. Several of these variations are shown on the plates for comparison with unusual trails of *Paramphibius*.

The simple feet were worked peristaltically as a unit and the maxillipeds used in their pushing function more or less in unison. Sometimes there was a slight tendency to pace with the braces of simple feet or the maxillipeds, but this usually occurred when the organism was wandering circuitously.

In burrowing forward a record of disturbed mud, an occasional *Cruziana*-like fanning of the mud (pl. 12, figs. 2, 6) in the midst of the burrow where the going became difficult, and at the end, the arcuate impression of the front of the cephalothorax are about the only telltale tracks. The maxillipeds appear to be of as great importance as the chief organs of propulsion in this type of locomotion as in walking on the surface. The telson is also usually much used in this action. But, as Owen (1873), Woodward (1878) and others have pointed out, the plowshare action of the great cephalothoracic shield is probably of principal importance here.

When disturbed in the midst of walking on the surface, or when stranded by the tide on the beach (Patten and Hitchcock, 1908) *Limulus* digs in vertically with surprising rapidity. In this activity the maxillipeds play the most important function of excavation while the simple feet busily push the mud and sand back to the maxillipeds for removal. Lloyd (in Owen, 1873) called attention also to the fanning of the gill books in removing finer detritus in this operation. Lloyd also observed that the maxillipeds may operate in unison or alternately in this excavation, but he neglected to mention the important part played by the simple feet in this sinking operation. The resultant excavation is roughly comparable to the impression made by a cloven hoof in the mud. It recalls very forcefully the Paleozoic "fucoids" known under the form-genus of *Cruziana*, some of which Abel (1935, pp. 271–275) and Fentons (1937) have shown pretty clearly to have been made by trilobites. Plate 12, figure 2, shows such a "*Cruziana*" pit made by a young *Limulus* in mud when annoyed by having several drops of fresh water splashed on it. Similar "fucoids"

have been found associated with Devonian casts of *Protolimulus*, and certain indefinite mud masses associated with *Paramphibius* suggest such an origin.

The varied use of the telson creates many characteristic trail markings which are quite unmistakable. Plate 12, figure 4, shows the marking made by young *Limulus* on rather stiff mud when its ventral moisture had been exhausted and it began to feel itself sticking to the mud. In several of the *Paramphibius* tracks shown on plates 1 and 3 very similar impressions are recorded. Abel (1935) has also vividly described a similar disaster which overtook the Jurassic *Limulus walchi* of the Solnhofen beds. It is an interesting side light that these Jurassic trails were first attributed to vertebrates. It seems to be almost inevitable that arthropod trails, and especially those of limuloids, should first be interpreted as of vertebrate origin! In this case cited it was Abel (Lebensbilder aus der Tierwelt, 1st ed., 1921 (1922), p, 461; and Vorzeitliche Lebensspuren, 1935, pp. 267–275) who first presented the undoubtedly correct interpretation of the trails which T. C. Winkler (1886, p. 241) described as those of *Pterodactylus kochi*, an interpretation in which J. Walther (1904, pp. 152, 204) concurred, but which Franz Baron Nopsca (1923) rejected in the main body of his great work on the families of reptiles, preferring the interpretation of the track as the resting imprint of an *Archeopteryx;* in the supplement, however, he concurred with Abel in viewing the trail as that of a *Limulus walchi*. The use of the telson in righting an overturned crab can be amusingly demonstrated by any visitor to the seashore where king crabs occur.

In simple walking the tail was little employed, and even for the very frequent feelinglike action of superficially inserting the front edge of the prosoma in the mud as the first step in burrowing, no use was made of the telson. When sinking vertically in the mud after the manner brought out by Lockwood, Dawson, and others, the tail is occasionally lashed from side to side as though clearing away the debris pushed out from beneath the carapace. This is well brought out in the seashore photographs taken by Doctor Patten (fig. 4, d). (Compare figs. 1, 2, 4, pl. 13; figs. 1, 5, pl. 12, with fig. 3, pl. 3, and fig. 3, pl. 5.)

FIG. 4.—*Limulus polyphemus* on the Atlantic coast during the spring mating season. Photographs a and b show two pairs in nuptial embrace, stranded at low tide. The male is usually smaller than the female, as in fig. b, and often rides to shore clinging to the buckler of the female. Photograph c shows the mating in progress at low tide in a small tidal pool. Actual egg-laying in progress. Photographs d and e show tracks made on the same beach where photographs a and b were taken. Such trails occur by the thousands along the shore during the brief mating season. Fig. d shows a crab in the process of sinking vertically into the damp sand. Of particular importance in this action is the flaying action of the telson by which the sand removed from under the venter by the simple feet and pushers is distributed laterally. Photographs a and b and d and e were taken along the Atlantic coast by the late Wm. Patten, of Dartmouth College. Prints made through the courtesy of the Department of Evolution, Dartmouth College. Fig. c was taken April 10, 1936, at St. Petersburg, Fla., by Dr. H. G. Richards, of the New Jersey State Museum, Trenton, N.J.

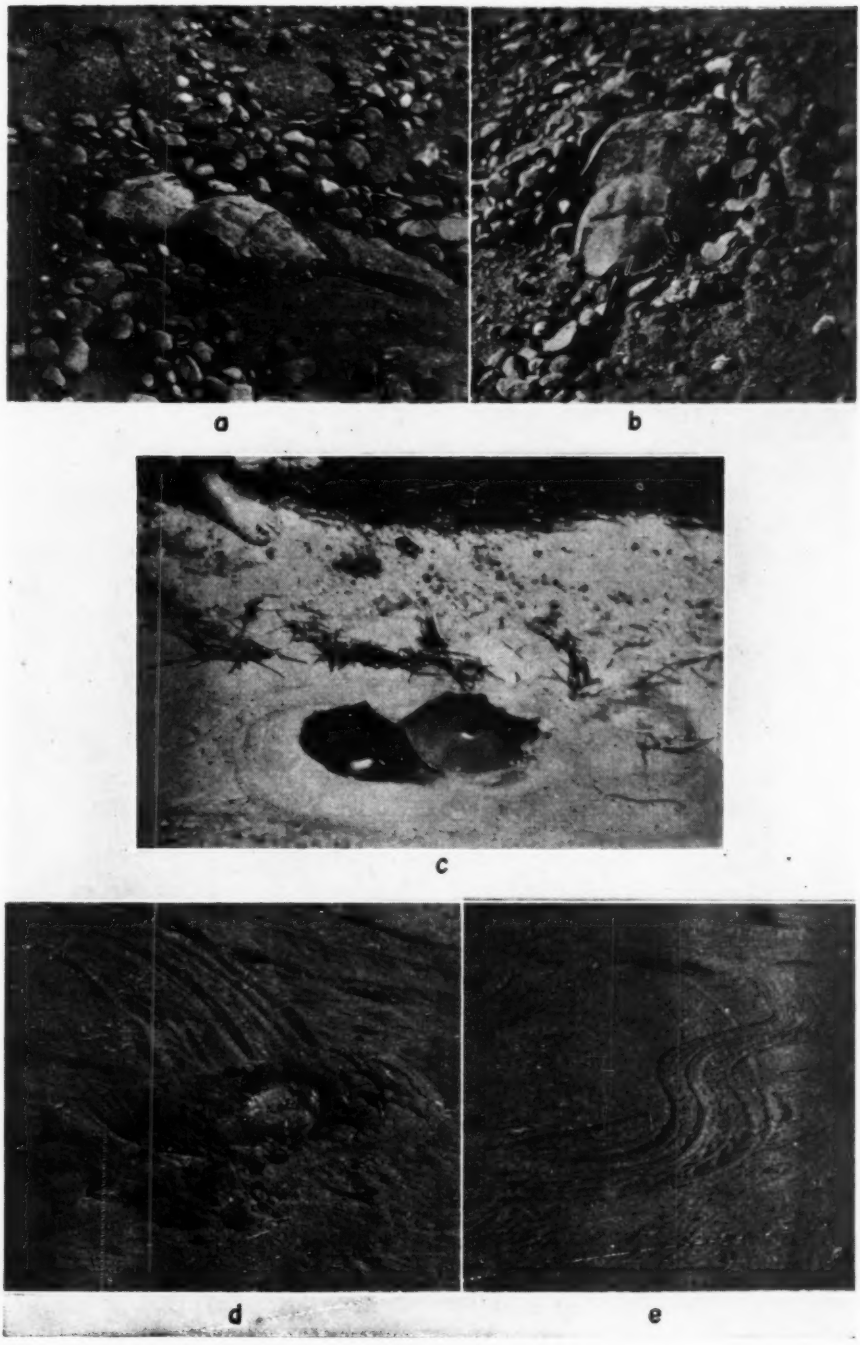

FIG. 4.—(*See opposite page for legend*)

Burrowing, then, appears to be the normal habit of *Limulus*, whereas walking is chiefly a seasonal event which is principally restricted to adult crabs during the mating season. The photographs shown in fig. 4, *d*, of seashore trails taken by the late Professor Wm. Patten are of stranded crabs on a sand beach during the mating period. Figure 4 shows three pictures of mating pairs in tidal pools. We learn that many of the trails of *Limulus* during this period are double, or unusually deeply impressed or partially obliterated as though it was a record of a beaten path. These anomalies are due to the curious habit of the crabs to seek the shore in pairs, the male often hanging onto the tail of the female, or several males clinging one behind the other, a female in the lead (Arnold, 1916, pp. 294, 295). In other cases, and more commonly, the male grasps the female with modified antennal chelae and rides in on her back, thus accounting for the unusually deeply impressed tracks in some trails. Owen (1873, Woodward, 1878, p. 231) has described this mating custom as follows:

> In spawning season the female laden with eggs not only walks to shore, but carries on her back the salacious male holding on firmly to her carapace by his specially modified antennae.

It is likely that in this seasonal nuptial walk of modern *Limulus* lies the explanation of the abundance of walking trails of *Paramphibius*, almost to the complete exclusion of other types of trails, and also the recurrence of trails of the same type leading each time in the same direction. Apparently *Limulus* feeds little, and certainly is not easily frightened during this brief season of pressing necessity. The "polyandrous" habit of *Limulus* may also explain the "beaten trails" found associated with the simple trails of *Paramphibius*, and the habit of the female to carry the male in to shore on her back may explain the deeper impression of some of the trails such as shown on plate 2, figure 3. It is also likely that some of the variation in size of the larger trails may be sexual, for most of the adult males of modern king crabs are smaller than the females.

Locomotion of Paramphibius.—Quite independently of the experimental data obtained in the study of *Limulus*, and even before that study was undertaken or the method of locomotion of the king crab was entirely clear, the essential characteristics of the locomotion of *Paramphibius* were worked out from the very perfect trails. When finally the locomotor habits of *Limulus* were studied, they were found to be essentially a living diagram of what had been previously a hypothetical scheme. The Lanesboro trails presumably show an unusual concentration of *Paramphibius* trails made at regularly spaced intervals in at least two major occurrences. They record migration, not static dwelling. The organisms were essentially all walking in one direction (shoreward?). The trails were made in shallow water or on a recently exposed mud flat which was still moist. From trails such as that shown on plate 11, figure

7, it would appear that some of the trails were made by a half-swimming, half-walking animal after the manner commonly observed in the case of limuli in aquaria. Such trails are made up of shallow ripples appar-

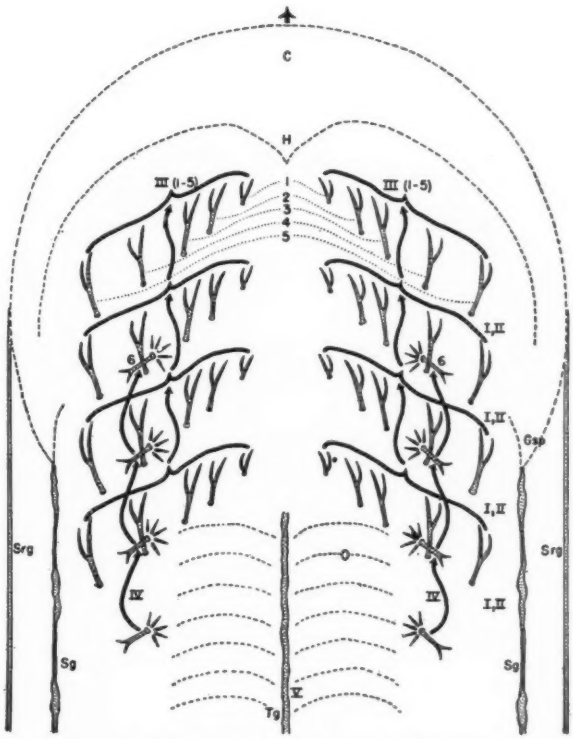

FIG. 5.—Schematic diagram of the walking trail of *Paramphibius*. Trail synthesized from specimens in University of Cincinnati Museum. Interpretation based in part on observed locomotor habits of *Limulus polyphemus* when walking on wet mud. Stages in locomotion: I—Cephalothorax uplifted, front first and highest; genal spines (Gsp) touch mud. II—Maxillipeds extended and anterior feet (1–5) dislodged from front to rear; cephalothorax and appendages carried forward, genal spines usually grooving the mud on either side of trail (Sg); grooves deepest when cephalothorax held highest anteriorly at outset of stage I. III—Cephalothorax lowered; walking legs (1–5) placed essentially peristaltically opposite each other by pairs from front to rear, chelae spread; antennules apparently imprinted only by accident. IV—Maxillipeds (6) freed from mud, flexed, with pusher blades extended and terminal segment bent backward; pusher imprinted in mud usually as a surcharge upon the immediately preceding tracks of the anterior maxillae. V—Extension of maxillipeds, pushing with imbedded pusher, and brace of simple feet. Head raised (I), tail dragging (Tg) the while to make a more or less continuous furrow; "sleigh-runner" (Srg) made if head not lifted high enough to clear surface; "holding-border" (H) bracket may also be occasionally impressed in the track series, if head sinks unusually low in mud; gill books and operculum (o) may also leave faint tangential record. (VI—When needed, telson may be used as a pushing organ and also the buckler by inflection; these are auxiliary to the operations of the circumoral appendages, however, in walking on the surface.) C—Position of the cephalothorax at most forward position indicated here; Gsp—Position of genal spine; 1, antennules; 2, antennae; 3, mandibles; 4, 5, maxillae; 6, maxillipeds. Drawing by A. S. Caster.

ently formed by the fanning of the gill books and operculum, with occasional scratches or lone impressions of simple feet. Occasionally in such trails only the impression of the maxillipeds is preserved, as though they had been used to speed up the swimming. In still others, only the balancing groove or interrupted depressions made by the telson are associated with the ripples. In some places the grooves or interrupted footprints alone record this type of progression. Some of these variations are shown on the plates.

The walking habits of *Paramphibius* have been summarized diagrammatically in figure 5. Walking apparently consisted in hitching along in the limuloid manner. Starting with all feet in the mud and the carapace essentially free of the surface except for the telson, which may have been uplifted too at the time, walking was essentially as follows: The headshield was raised, and the braces of simple feet were simultaneously raised from the surface and extended forward. Then the maxillipeds or pushers, which had been thus far flexed, were straightened and the whole organism moved forward correspondingly. Then more or less peristaltically the simple feet were implanted in the mud from front to rear, tips first, and flattened as the weight of the organism was shifted to them. Then the buckler was inflected, the telson also drawn forward, thus raising the posterior part of the prosoma so that the maxillipeds could in the same movement be freed and moved forward and emplaced in a flexed position. Then again the prosoma was uplifted and aligned with the abdominal segments, the simple feet freed of the mud, extended forward, and at the same time the maxillipeds straightened to push the animal forward the length of a hitch. The prosoma was lowered, simple feet emplaced, buckler inflected with the bracing support of the telson, either at its base or if need be with its tip, and the maxillipeds being freed, were emplaced forward at about the position of the imprint of the previous fourth simple foot track.

In normal walking, only the posterior three pairs of simple feet were ordinarily employed. Occasionally, by accident or otherwise, the antennae were used, and rarely, seemingly by accident, the apparently dangling antennules or prostomal feet left their imprints as paired scratches when the organism sank unusually deep in the mud. On curves especially the imprints of the braces of simple feet and the pair of maxillipeds may be staggered as though the animal were pacing in a tetrapod manner. It was natural in rounding curves that the feet on the outside would be more widely placed than those on the inside. Where the animal pushed ahead with its "head" too highly uplifted, the postlateral extensions of the prosoma (genal angles) tended to drag, thus forming parallel grooves just outside the footprints (fig. 5, Sg). In some individuals the cephalothorax was so little uplifted that the ventral lateral portions of the head shield rode along in

the mud like sleigh runners after the manner of adult limuli (fig. 5, Srg). In many trails, these additional markings are discontinuous; in a few, one or the other type continuous, and some, both types of parallel furrows are intermittently developed after the generalized manner shown on figure 5. On curves the rigid body usually careened so that the head shield left a furrow on the inside of the curve. Sometimes the animals apparently nearly overturned, for the whole set of tracks on the outside of the curve will occasionally be omitted. This is exactly as in *Limulus*. When bogged down in the mud, as shown on plate 3, figure 2, *Paramphibius* lashed out with all appendages and the telson. The result was a chaotic track record, which recalls vividly the similar record recorded by Abel, 1935, for the limuli of the Solnhofen Plattenkalke. Occasionally *Paramphibius* went forward with its body apparently oriented in an anterolateral position in much the same manner as does modern *Limulus*, which I have likened to the curious sidewise running so often seen in dogs (pl. 5, fig. 2).

In *Paramphibius* the telson seems to have played a very minor part in walking, for in this operation it usually dragged behind (fig. 5, Tg, and pl. 10, fig. 6), was lifted up and down periodically (pl. 5, fig. 3), or was wagged from side to side. In freeing a stuck animal it was of considerable importance (pl. 8, figs. 1, 3) as in modern king crabs and in the Solnhofen limuli. Impressions of the edge of the operculum are sometimes preserved (fig. 5, o; pl. 9, figs. 2, 5) and possibly ripples made by the gill books, but so far as walking is concerned, these impressions were accidental. Occasionally the anterior rounded or plowshare border of the prosoma was imprinted and the imprint partly defaced as the animals momentarily yielded to the temptation to dig into the soft mud (fig. 5, c). The so-called holding-border, just anterior to the mouth and prosomal appendages, was also occasionally imprinted when the animals sank unusually deep or rested for a moment (fig. 5, H; pl. 9, figs. 3, 4).

Summary discussion.—In trails, locomotion and ventral anatomy, *Paramphibius* and immature king crabs are remarkably alike. The chief difference in the appendages is that the pusher is four-bladed in *Limulus* and five-bladed in *Paramphibius*. This really is not significant when the wide variation of the pusher in modern *Limulus* (American and Moluccan) is considered. Reports of five blades for the modern forms are common, although the writer has never seen a specimen of modern *Limulus* showing other than four pusher blades. In the termination of the maxillipeds by pseudochelae, both jaws of which are movable, the Devonian trail maker and modern *Limulus* are identical. However, there may be a modern tendency for the terminal portion (dactylus and spines) to break off in adulthood, if current accounts of the pusher blades terminating the maxillipeds are accurate. Many dried specimens in the laboratory do show this condition,

but the writer has never happened to see it in pickled specimens or live individuals. The Devonian forms apparently walked with the distal joint of the simple legs flexed, or flat-footed, thus impressing the whole chela in the mud, but modern crabs in adulthood appear to have a stronger palpal-propodal articulation, which permits them to "toe dance" on the tip of the chelae (e.g., plate 13, fig. 7).

If the interpretation of the markings shaped like terminally inverted printers' braces is correct, it would appear that the holding border (Woodward, 1878) of *Paramphibius* occupied a flatter under surface of the cephalic shield (doublure, Hall, 1888, p. 153) than in modern *Limulus* (fig. 2, Hb), where this surface is dorsally arched. The frequency with which the brace marks occur in the *Paramphibius* trails would seem to require some such explanation. In *Limulus* the holding border leaves its impression only when the animal dies, or rests for an abnormal time in the yielding mud (pl. 12, figs. 2, 6).

The grooves outside the main trail of *Paramphibius*, which have been compared with similar structures made by the "genal spines" of *Limulus*, are proportionately a little farther from the tracks than in *Limulus*. It is probable that these spines in *Paramphibius* protruded slightly posterolaterally from the general marginal rotundity of the "sausage cutter" prosoma (Lockwood, 1870). The broad mesial chevron markings of the trails, which are apparently the impressions that Willard (1935) attributes to ventral armor, are similar to the impressions of the coxognaths of *Limulus*.

The telson of *Paramphibius* may not have been as attenuated as in *Limulus*, but it seems to have been similarly trigonal in cross section and ventrally flattened. It is unwise, however, to draw conclusions on the nature of this organ too fully from the impressions or casts, as an examination of the trails left by the telson of *Limulus* will show. If the telson was distally up-bent, as is that of *Limulus*, then only a fraction of its total length is dragged or impressed, and the imprint gives a false impression of shortness and bluntness. Certainly this fallacious conclusion has marked the description of the type of *Protolimulus*, and may give a false impression of *Paramphibius*. However, the telson impression of *Paramphibius* usually has the general ensiform dimensions of a modern *Limulus* tail and may give a true mold.

COMPARATIVE PALEOICHNOLOGY

Since there is such a close similarity between the trails of *Paramphibius* and modern *Limulus*, the next question that arises is how do the trails of *Paramphibius* compare with the trails of fossil arthropods and merostomes? Especially, how do they compare with those of the Xiphosura Limulida?

Biramous impressions of the sort made by the simple feet of *Paramphibius* and modern *Limulus* are a characteristic structure among the several groups of arthropods. The Ordovician trails (*Asaphoidichnus*

and *Teratichnus*) described by Miller (1880) as those of trilobites, have been compared with those of *Paramphibius* (pl. 10, figs. 1–4). The Ordovician trails are made up of braces of simple biramous impressions, which are remotely comparable with the five simple footprints of *Paramphibius*. These trilobite tracks show no heteropody, but some of them do show the curious record of the animal having occasionally moved forward with its feet all oriented in an anterolateral position, and of lashing out mightily with some of its appendages on curves or under other conditions tending to slow down progress. Roberts (1863) superficially described certain problematical trails from the Old Red Sandstone of Great Britain that resemble, insofar as one can tell from his incomplete description and figures, the simple footprints of *Paramphibius* (see his fig. 2). In the light of the findings of Nathorst (1881) on trails made by crabs and of Trustheim (1931) on trails made by Crustacea, and in the absence of heteropody, it would appear that Robert's trails were made by freshwater (?) crustaceans. Robert's trails may also show heteropody, if the indistinctly annular impressions (compare with pl. 10, fig. 1) he shows have been rightly interpreted by Størmer (1934). Inasmuch as heteropody is the most characteristic feature of the tracks of *Paramphibius*, it seems safe to eliminate trilobites, insects, and other nonheteropodous arthropods from consideration.

A great many trails from early Paleozoic to the present that show a heteropodous condition of the tracks have been assigned to the arthropods. Dawson (1862–1890), Nathorst (1881), and Hall (1852), as well as many others since the middle of the past century, have contributed largely to this interesting field of problematical paleontology. Several trails assigned to the form genera *Merostomichnites* (Matthew, 1909), *Idothea* (Kier, 1911, 1924), and *Protichnites* (Sharpe, 1932), and others show two types of tracks in a single trail. These form genera have usually been assigned to merostomes of one type or another (Sharpe, 1932; Nathorst, 1881; Kier, 1911, 1924; Størmer, 1934). This is not the place to discuss the assignments, but it does appear that several of these Paleozoic trails were made by eurypterids or related merostomes. It seems certain from such evidence that the differentiation of the locomotor appendages of the merostomes into pushing and walking legs occurred at a very early date. In several of the trails illustrated by Hall (1852, pp. 35–37, pl. 15, figs. 1–6; pl. 16, figs. 1–4; pl. 13, fig. 14) from the Silurian (Clinton) of New York, trails, which seem to have been made by merostomes (Packard, 1900, vol. 36, pp. 63–71), appear to show the impression of a four- or five-bladed pushing organ (particularly, idem, pl. 15, figs. 1–5; pl. 16, figs. 1, 2).

Through the kindness of Mr. F. H. Ward, of Ward's Natural Science Establishment, in Rochester, N. Y., I have been able to examine the C. J. Sarle (1906) collection of Silurian ichnological material, which includes

a considerable amount from the Clinton as well as valuable European specimens. In placement of the tracks, the Clinton trails are very similar to the straight-away trails of *Paramphibius*, in which the tracks are opposite one another. Several of these trails will be the subject of a separate paper, now in preparation.

Climactichnites and *Protichnites* of the Ozarkian Potsdam sandstone, subjects of a long-continued controversy (for literature see Burling, 1917), need not be discussed here because they are probably of gastropod origin (Raymond, 1922, Abel, 1934, pp. 242–249, and others). They were interpreted as arthropods by Dawson (1862–1878), who experimented with trails of *Limulus*—an interpretation concurred in by Logan and Owen (1852), Billings (1870), Packard (1900), Patten (1908), Walcott (1914), and others. *Idothea baltica* Pallas (Nathorst, 1881) shows, in addition to heteropody, a placement of the simple feet highly comparable to the braces (or chevrons) in *Paramphibius* (Abel, 1935, p. 252, fig. 220). The form genus *Idothea* is probably of eurypterid origin. The large trails (*Protichnites gallowayi*) described by Sharpe (1932) from the vicinity of Roundout, N. Y. (lower Middle Ordovician), show heteropody, chevron-like placement of apparently nonchelate simple feet, and curious "cloven" pusher (?) impressions of much larger size, which lie outside the alignment of the impressions of the simple feet. These may well have been made, as Sharpe suggests, by specialized merostomes of the Ordovician (eurypterids or forms not yet well known), but, in view of their arthropod origin, seem questionably assignable to the form genus *Protichnites* (Logan and Owen, 1852). Sharpe thought *P. gallowayi* was made by an Ordovician eurypterid, but, owing to the specialized nature of the trails, Størmer (1934) felt that they were probably not of eurypterid origin. *Merostomichnites strandi* Størmer (1934) from the Downtonian of Spitzbergen is a heteropodous trail showing a curious "annulated" four- or five-clawed (?) impression associated with simple tracks, which have the appearance of having been made by the tri-partite distal ends of simple walking feet. (Compare Størmer's figure with pl. 10, figs. 1–4, and pl. 13, fig. 3 of this report.) The "annulated" impressions are in series with the simple tracks and may have been made by a modified "pusher." Similar "annulated" markings appear on the slabs with the trails in the Old Red Sandstone described by Roberts (1863), but their relation to the simple tracks (scratches) was not clear on his material. Størmer thinks that the Spitzbergen trails were made by eurypterids. The organization shown by the Devonian *Paramphibius* trails seems to fit the general pattern of American and European trails from the Ordovician and Silurian that have been assigned to the merostomes.

Trails that bear considerable resemblance to *Paramphibius* have been described from the Devonian and more recent strata. Packard (1900) described *Merostomichnites*

beecheri from the Upper Devonian (Conewango) of northwestern Pennsylvania and said that C. E. Beecher concurred with him in interpreting the trail as made by a partially swimming merostome, which careened slightly so that the appendages of one side were forced a little more deeply into the bottom mud than those of the other. Only the leg imprints are preserved, and these are not definitely chelicerate. Moreover, there is no indication of heteropody in the trails that Packard described. However, modern *Limulus* frequently leaves almost precisely the same kind of record when progressing in this intermediate manner. Very similar impressions are common in our *Paramphibius* material also. Figure 6 shows the locality of *M. beecheri* and figure 9 the stratigraphic horizon compared with that of *Paramphibius*. It seemed significant to Packard and Beecher that *M. beecheri* occurs in the same general locality and at essentially the horizon of *Protolimulus eriensis* (Williams), (*Prestwichia*, Williams, 1885; *Protolimulus*, Packard, 1886), in the Conewango series. *Prestwichia randalli* Beecher (1902), (*Paleolimulus? randalli* (Beecher), Dunbar, 1923), also occurs at this horizon.

While conducting a field trip into the oil region of Pennsylvania during the field season of 1935, the writer, accompanied by Dr. Bradford Willard and other colleagues who were holding a conference on Devonian stratigraphy in Allegany State Park, New York, found on the under side of a sandy conglomerate in the Conewango series (Pope Hollow conglomerate, Salamanca suite) at Pope Hollow, Cattaraugus County, New York (see Caster, 1934, for stratigraphy), several chelicerate tracks and trails much resembling in organization *Merostomichnites beecheri* and in detail the simple tracks of *Paramphibius*. Three casts of *Protolimulus* have been recovered from this conglomerate by the writer during the past eight years. Throughout the Conewango series in the Warren-Bradford area in Pennsylvania, the casts of *Protolimulus* are common; especially is this true for the basal (Panama-Wolf Creek) and mesial (Salamanca) sandstones of the series. During the summer of 1936 the writer discovered several *Merostomichnites*- and *Paramphibius*-like trails in the Conewango near Ridgway, Pa., in association with casts of *Protolimulus*. In all the *Merostomichnites* trails from the Conewango series, the impression of the pusher blades of maxillipeds is obscure, but the record of chelicerate endognaths as well as telson impressions comes out very clearly in many of the trails. Several workers have doubted the possibility of late Paleozoic Xiphosura being able to make tracks of the size left by *Paramphibius*, and as a consequence have urged that either an eurypterid or scorpionid be sought. It is found upon very painstaking comparisons that the transverse dimensions of *Protolimulus*, *Paleolimulus randalli* and the unidentifiable indistinct *Protolimulus* casts exactly conform to (1) the trails of *Merostomichnites beecheri*, (2) to the new

xiphosuran trails from the Conewango herein reported, and (3) to the trails of *Paramphibius*. Moreover, E. R. Eller reports (personal communication 1936–37) new xiphosuran remains from the Conewango series and from the beds lying between the Conewango and the Lanesboro horizon. These also are of exactly the dimensions to have made either type of track. Moreover, the writer is unaware of eurypterid remains from the Upper Devonian that would indicate an adult *small* enough to have made the tracks of *Merostomichnites* or *Paramphibius*.

Since this study began very similar trails from the Mississippian and Pennsylvanian have been reported at horizons from which xiphosuran material has been derived. No opportunity has yet been afforded to verify these reports. *Protichnites carbonarius* Dawson (1873, 1878), from the Carboniferous of Nova Scotia is too indistinct and unsatisfactory to warrant consideration now. The problematical nature of these tracks was brought out by Packard (1900). Some of the Nova Scotia trails described by Dawson and also by Matthew (1889, 1909) were presumably of arthropod origin, but like so much of the Paleozoic ichnological material, the Acadian records were poorly preserved or very incomplete. The trails described by Topelman and Rodeck (1936) from the Pennsylvanian of Colorado, seem, as can best be judged from indistinct text figures, to be merostomaceous but are more likely the trails of a scorpion. They apparently do not show heteropody of the type seen in *Paramphibius*, although there is a suggestion of pushing by some of the feet. The feet were apparently not chelicerate, and the placement of the feet was clearly dissimilar to that of *Paramphibius* or *Limulus*. Trails of neither the indistinctly known *Paleolimulus signatus* (Beecher), Dunbar (1923, *Prestwichia signatus* Beecher, 1904) of the Kansas Permo-Carboniferous nor of the well-preserved and carefully studied *Paleolimulus avitus* Dunbar (1923), of the Kansas Permian, have been reported. The anatomy of *Paleolimulus avitus*, as brought out by Dunbar and discussed below, indicates that the genus was certainly capable of making either *Merostomichnites*- or *Paramphibius*-like tracks and trails. In this genus the presence of a whorl of maxillipedal pushers is established beyond controversy. There are undoubtedly many more records of Paleozoic xiphosurous trails, but they have escaped my attention.

The world-famous trail records of *Limulus walchi* in the Jurassic Solnhofen Plattenkalke of Bavaria merit closest comparison with the trails of *Paramphibius*. How unfortunate it is that so few of these trails (Abel, 1935, p. 267) which occurred in such amazing abundance (Walther, 1904; Abel, 1934) in the lithographic quarries have been preserved! Abel reports that specimens of the once commonplace trails are great rarities in the museums of the world. Now that lithography has fallen into desuetude, the quarrying has nearly ceased and the valuable records are lost.

EXPLANATION OF PLATE 1

FIG. *1*—*Paramphibius didactylus* Willard. Parts of two trails, one of which shows the impression of a full brace of five simple feet on the right side and four on the left. The secondary trail shows only the serial impression of one simple foot on each side and indistinct pusher impressions. ×1.

2-3—Details of the footprints (molds) of *Paramphibius*. *2* shows the serial impression of the same foot in three successive tracks. The bottom track is essentially the impression of the chela, whereas the succeeding tracks show a little posterior dragging. Note the molds of small mounds at the proximal ends of the three impressions. These are attributed to the mud filling of the distal articulation of the leg. *3* shows simple tracks of the kind that gave the original basis for assuming that the impressions were split to the base rather than chelate, as it now seems that they are. *2*×2; *3*×1½.

4—Serial impressions of the right pusher of a mature *Paramphibius* to show the variation in angle of placement. Middle tracks show well the impression of the terminal spines of the maxilliped. ×2.

5—Serial impressions of the left pusher of an immature *Paramphibius*, which illustrate the shorter "step" of the young organism, the proportionately shorter "heel-bar," and in the right track, the shorter terminal spines. ×2.

6—Maxillipedal casts of *Paramphibius*. Upper track shows the terminal spines of the maxilliped, both of which are movable. ×2.

All illustrated material on this and following plates is from the type locality for *Paramphibius* in the Kingsley shale (Upper Devonian) at Lanesboro, Pa., unless otherwise noted.

EXPLANATION OF PLATE 2

FIG. *1*—*Paramphibius didactylus* Willard. Trail of an immature individual, which shows a tendency (right side of picture) of the organism occasionally to walk on the ends of the simple feet as does modern *Limulus* (pl. 13). The chevronlike grooves are attributed to the dragging of the gnathobases. The deviation of the trail was apparently made to avoid a small depression in the sandy mud, or possibly represents a temporary resting place. Trail apparently made in wet mud subaerially. Lower left corner shows a trail of the same-sized individual in which the genal angles (or "sleigh runners") were dragged and possibly the operculum was repeatedly inserted in the mud in the manner of an ovipositor. Note mesial interruption of the winged braces. ×1.

2—Trail of a small organism, which demonstrates the type of trail in which the pusher tracks predominate and in which only half of each simple chela in most cases was scratched in the mud, thus leaving no trace of a split claw. ×1.

3—Mature trail showing clearly the serial impression of five pairs of simple feet and a pair of pushers. The unusually deep impression may be due to the excess weight of the male riding on the carapace of the female in the manner of modern king crabs during the nuptial walk. See also text fig. 4. ×1.

4, 6—Maxillipedal impressions showing characteristics of the immature pushers of *Paramphibius*. In *4* the fifth blade of the pusher is only very slightly impressed, thus giving a lopsided impression. Of particular importance here is the obvious ability of the terminal "heel" spines mutually to spread. ×2½.

5—Part of an incomplete trail of *Paramphibius* of the *didactylus* type, but in which the pushers are directed outwardly rather than inwardly, this being the left side of the trail (right not impressed, presumably due to careening of the organism). ×1½.

EXPLANATION OF PLATE 3

FIG. *1*—Parts of a discontinuous and circuitous trail made by an immature specimen of *Paramphibius didactylus* Willard. Compare the chevronlike pattern of the midpart of the track with the pattern made on sand by modern *Limulus polyphemus* (fig. 4, text). Note that the tail was not dragged in the part of the trail shown in the upper right but is clearly shown in the lower left, where it seems to have been serially uplifted and lowered, thus measuring its length successively in the mud. The terminal clot may represent the place where the animal temporarily rested, or sank vertically into the mud, or even was picked up by the incoming tide. ×1.

2—Mature trail of a *Paramphibius* made when temporarily stuck in the mud. Note the lashes of the simple legs and clots in the middle part of the trail where the animal

sank in deeply. Apparently the simple legs had considerable pushing ability in such an emergency. ×1.

3—Trail of an immature *Paramphibius*, which illustrates the serial application of the telson to the mud in walking rather than simple drag, which is much commoner. It illustrates also the serial drag of the genal spines (in series with the telson gouges) made as the body was pushed forward by the maxillipeds, prosoma uplifted and telson assisting in the action as a brace. It is probable that each pair of genal spine gouges was made synchronously with the tail-drag gouge immediately behind. ×1.

Explanation of Plate 4

Fig. *1*—Enlargement of a part of the trail shown on plate 1, figure *1*, to illustrate chelate nature of the simple footprints, five-fold nature of the simple tracks in each brace, and striking discordance in the direction of placing the simple feet and pushers. Note also the molds of small mounds of mud at the proximal end of each simple footprint. These seem to have been formed by contact of mud with the upright antepenult leg segment and the articulation between this segment and the chela. ×4.

2—Friction and contact markings which are commonly associated with the Lanesboro trails. This particular trail is unique in showing a more acute anterior angle of the "chevrons" than any others that have been observed. ×1.

3—A trail of the *P. didactylus* s.s. type showing the fortuitous nature of such incomplete trails. Compare with plate 2, figure *5*. Note also in this figure how variable the impression of the left (top) simple foot is from the left side of the photograph to the right. ×1½.

4—Part of a trail made by an individual temporarily stuck. The simple footprints are exceptionally weak and show filaments. The maxillipeds seem to have been of principal importance in freeing the organism. Compare with plate 3, figure *2*. ×1.

5—About half of a sigmoidal trail of *Paramphibius*, which is unusual in the almost complete absence of pusher impressions, although four pairs of simple feet leave their traces. Approximately ×½.

6—Under surface of a track-bearing stratum showing the characteristic depression (deformation, not scour) made by the organ (or organism) responsible for the "dumbbell"-shaped incisions which are commonly associated with *Paramphibius*. This is the bottom of the incision, and definitely the "tubes" on either end (the "bells") do not continue across to form a U-tube. The middle incision of this structure has been likened to the "Spreite" of *Rhizocorallium*. (See also pl. 11.) ×1.

Explanation of Plate 5

Fig. *1*—*Paramphibius didactylus* Willard. Part of a trail made apparently against a current or on a slope, which tended to divert the animal from the course it had set, as shown by the trend of the footprints on the right side toward the left and by the spread of the chelae on the left side. Note range in angle of chelae. ×1½.

2—A normal straight-ahead trail in which all of the simple feet tend to point to the right anterolaterally. Note also that the pushers in this trail seem to be counteracting this tendency by being directed on both sides in an anterolateral direction to the left. Note also impressions of five simple feet in several of the braces on the left. ×1½.

3—Trails of two immature individuals going in opposite directions, both using the telson very slightly as a pusher. Note especially that each impression of the telson shows a broad blunt end anteriorly. Apparently from the small clots of mud in the trail, the end of the organ was repeatedly inserted in the mud to give a slight prod or push, was then lowered its full length in the mud and drawn ahead, tip dragging, thus forming the central narrowest and deepest groove. ×½.

Explanation of Plate 6

Fig. *1*—Compound trail, which is unusually deeply impressed. So deeply are the pushers impressed (right side of picture) that the "heel" is bent backward nearly 130° and the pusher blades inserted very much as in modern adult king crabs. This trail may have been made by two animals walking in tandem fashion, or one carrying the other, the passenger occasionally letting down a foot to help push along. ×1½.

2—Immature *Paramphibius* trail, the axial part of which shows (middle of picture) some indistinct furrows that may have been due to the weak wave motion of gill books. The tracks are in a shallow depression on either side, which was possibly made by the lateral sliding of the prosoma. ×1.

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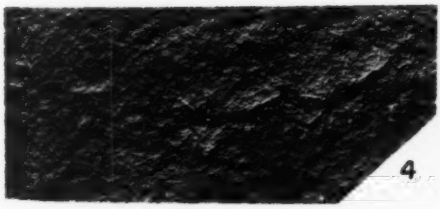

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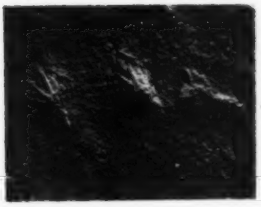

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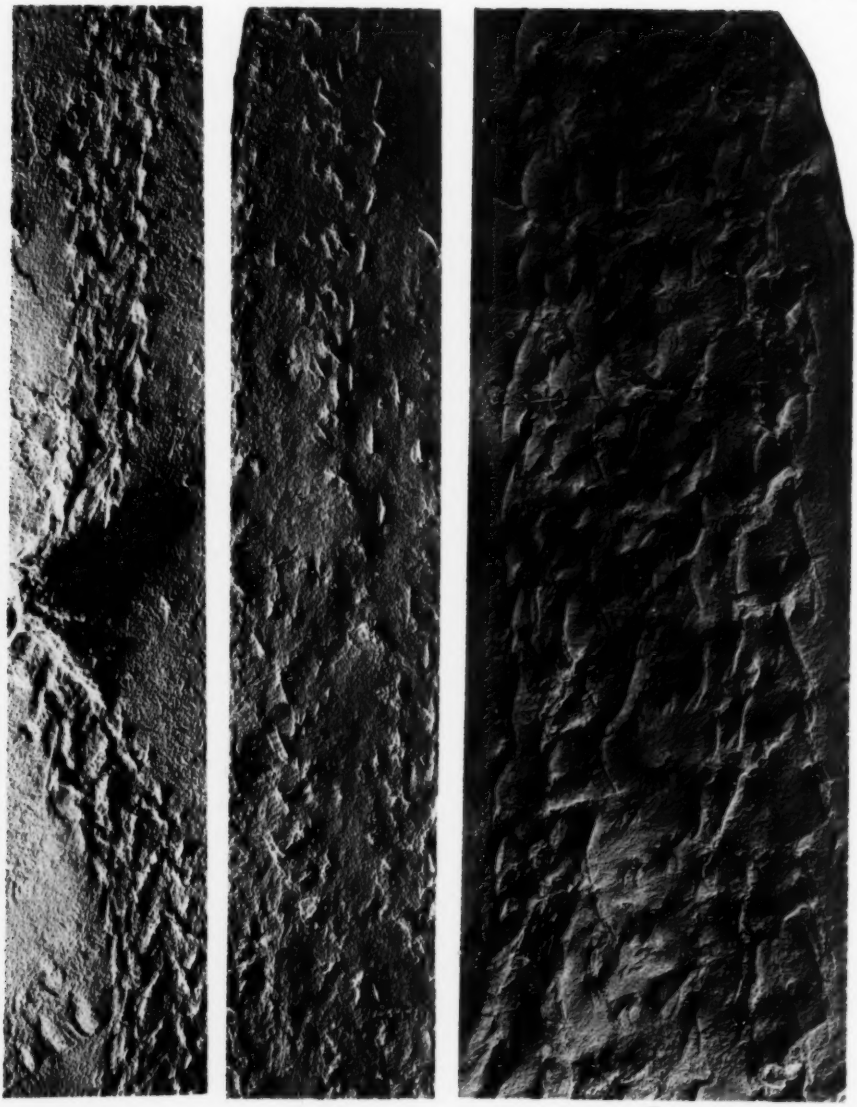
Caster, *Paramphibius*



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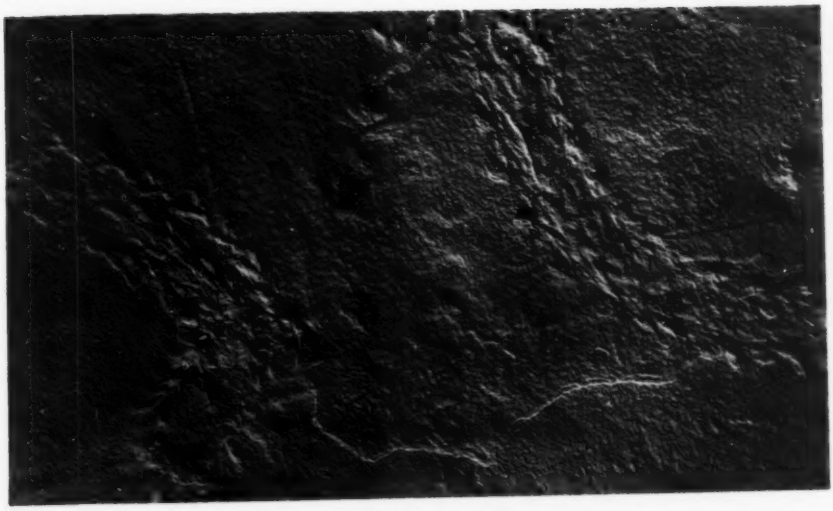

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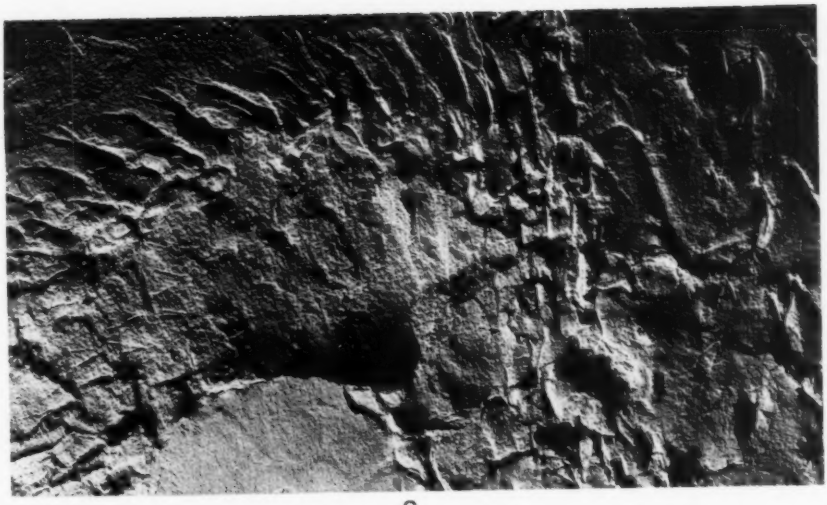

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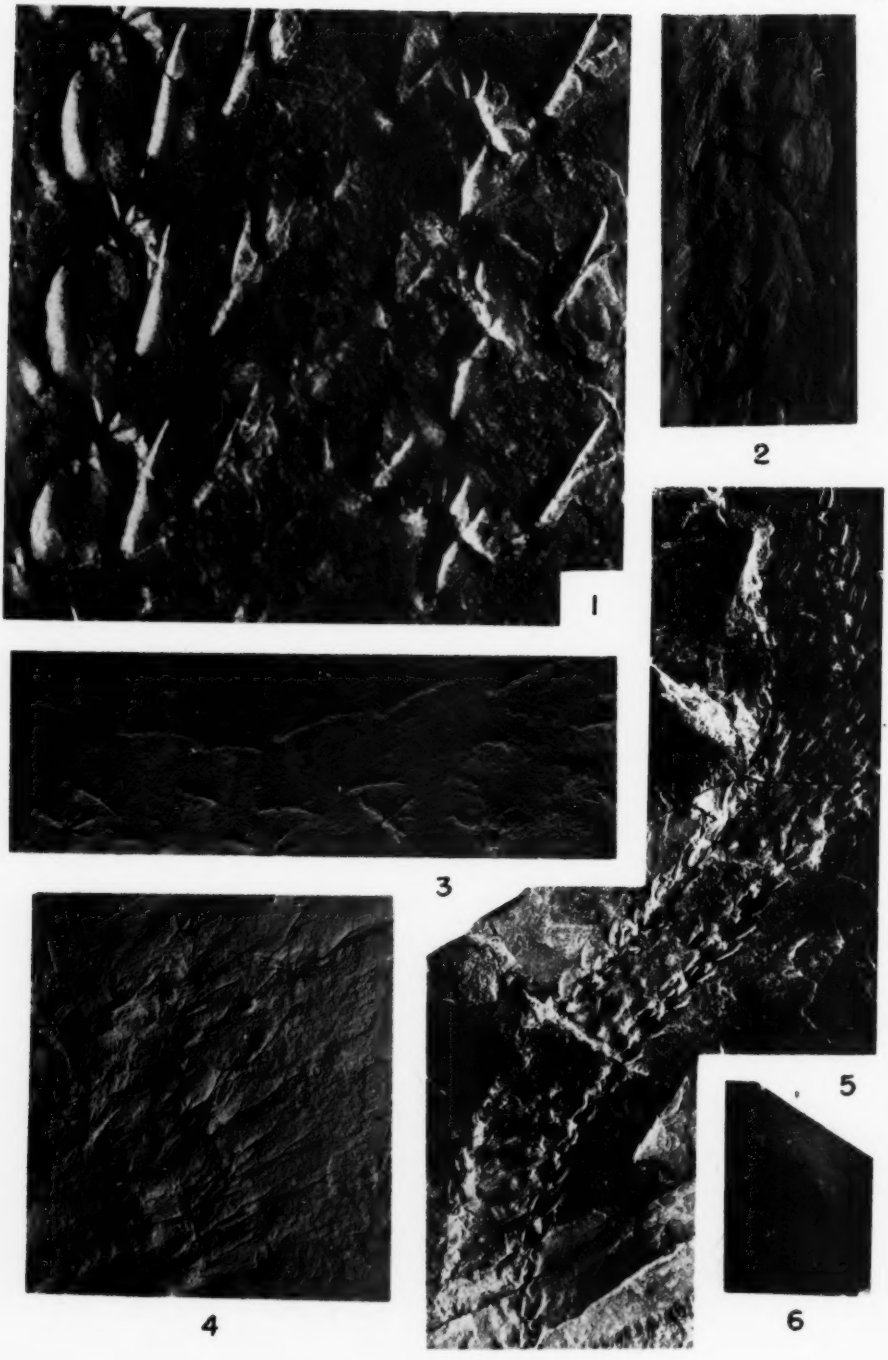

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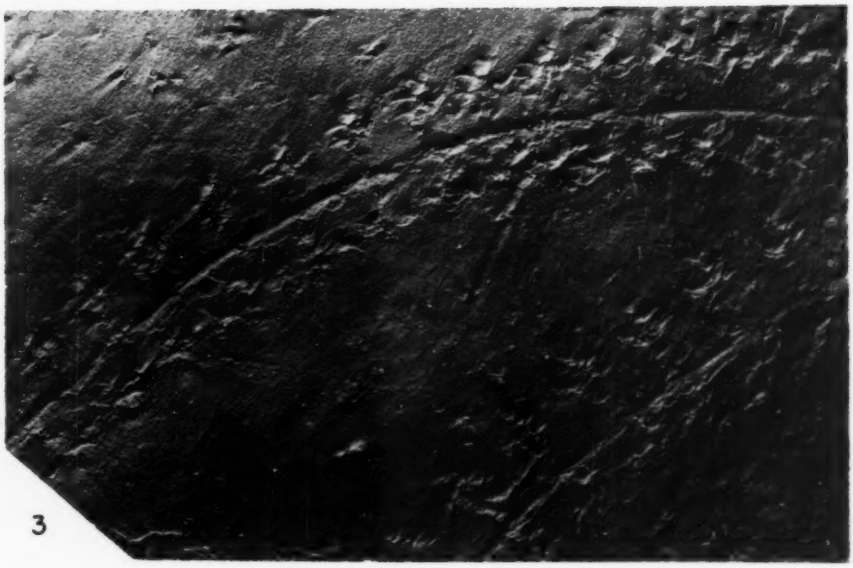

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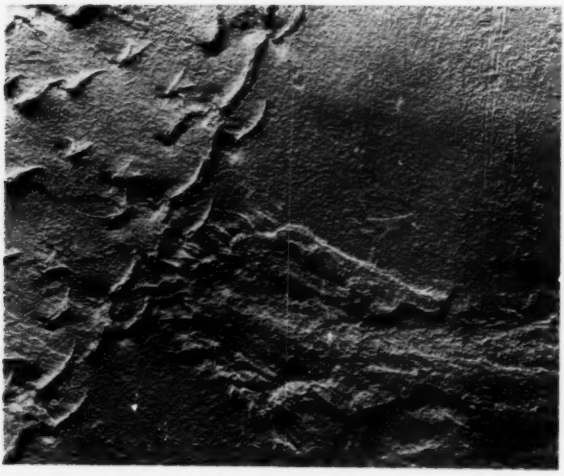

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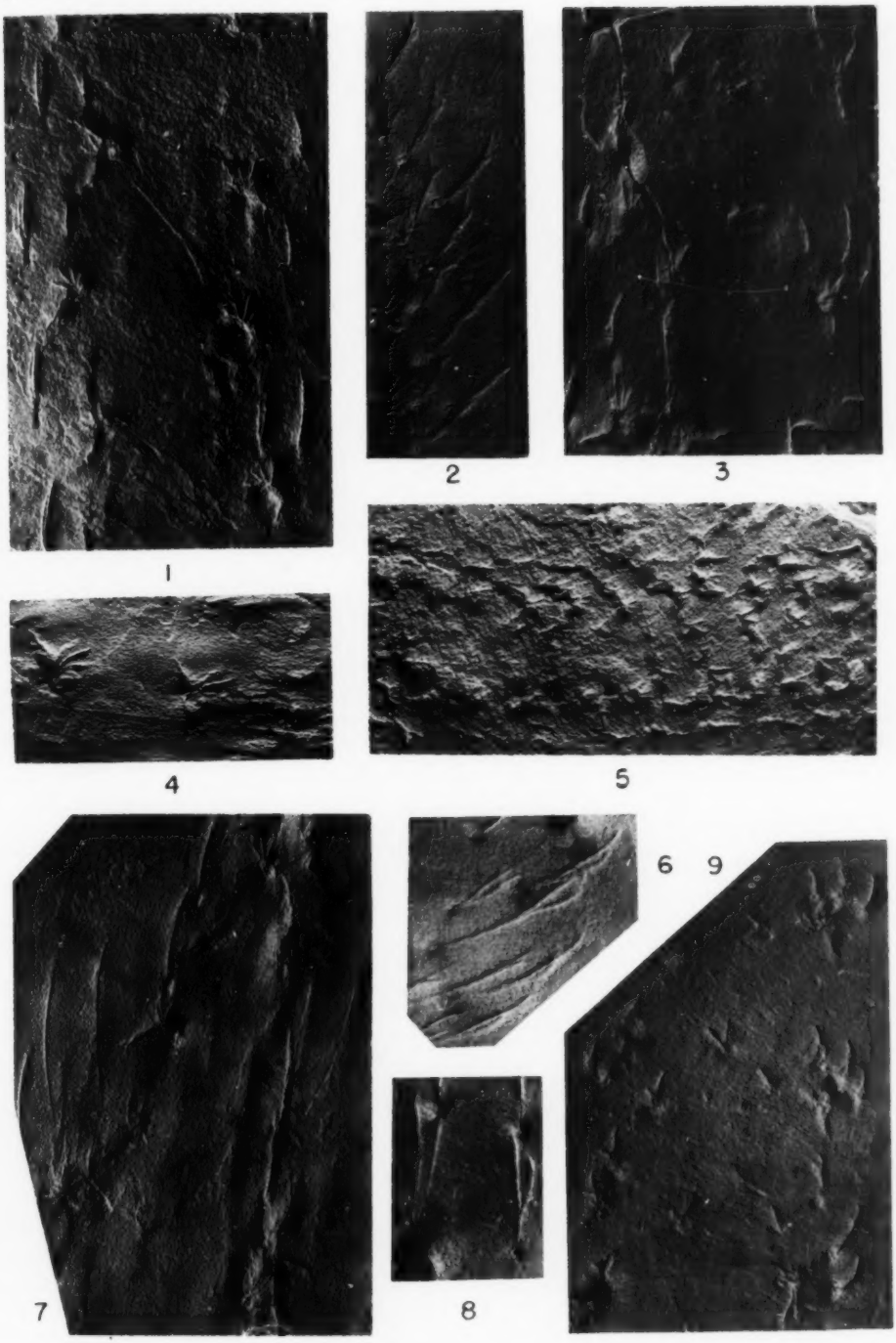

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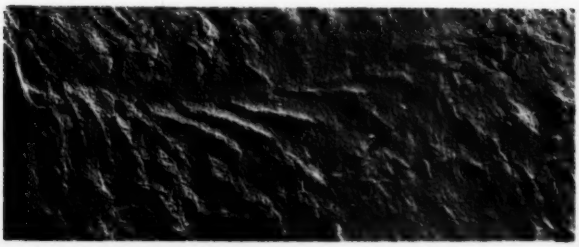

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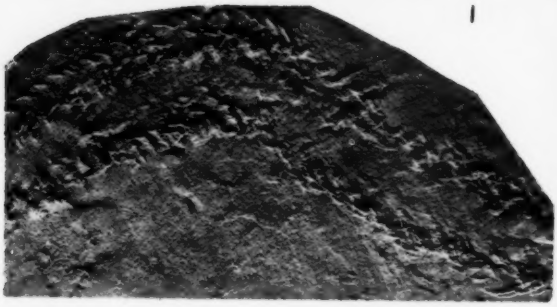

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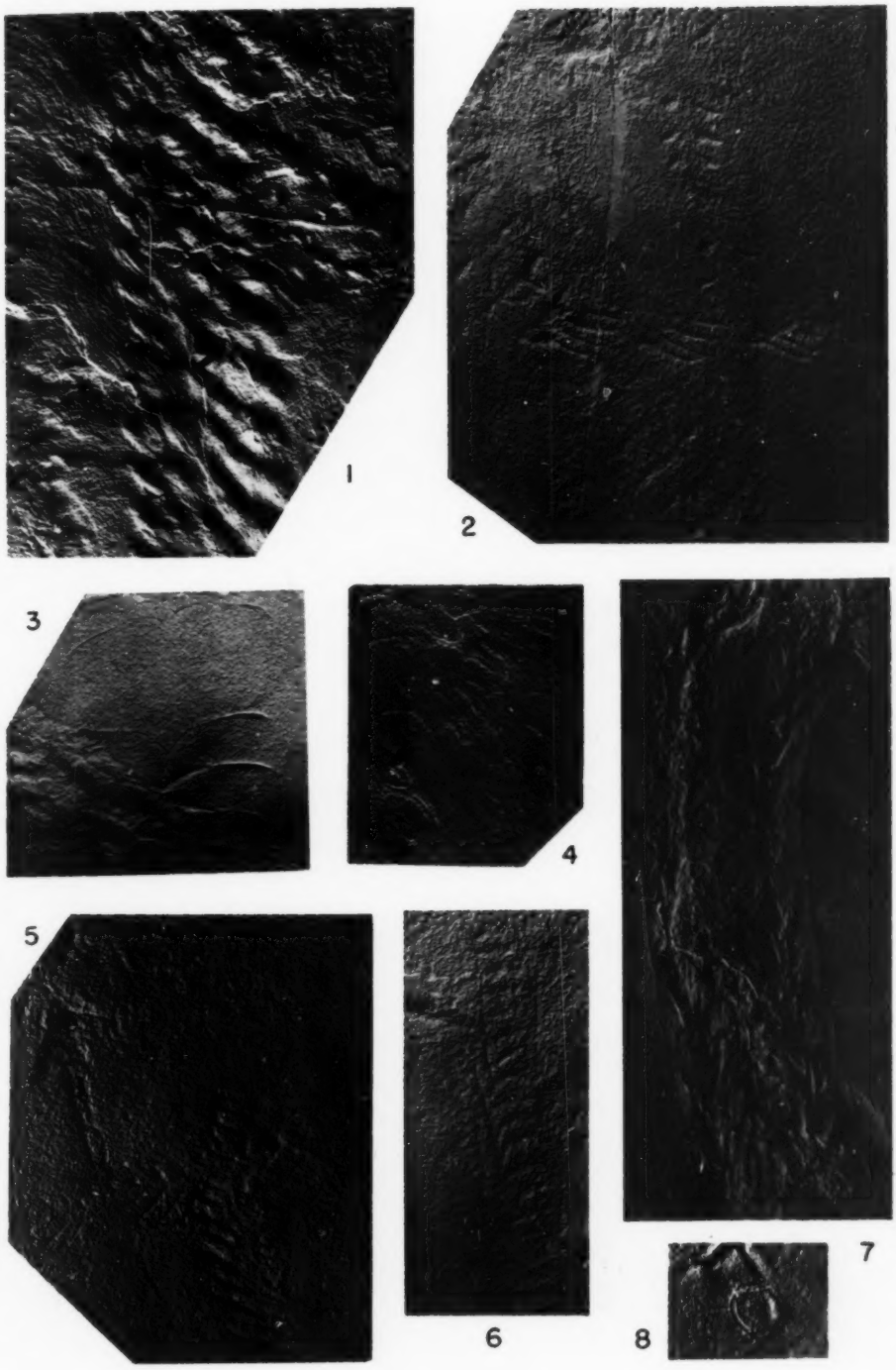
Caster, *Paramphibius*



Caster, *Paramphibius*

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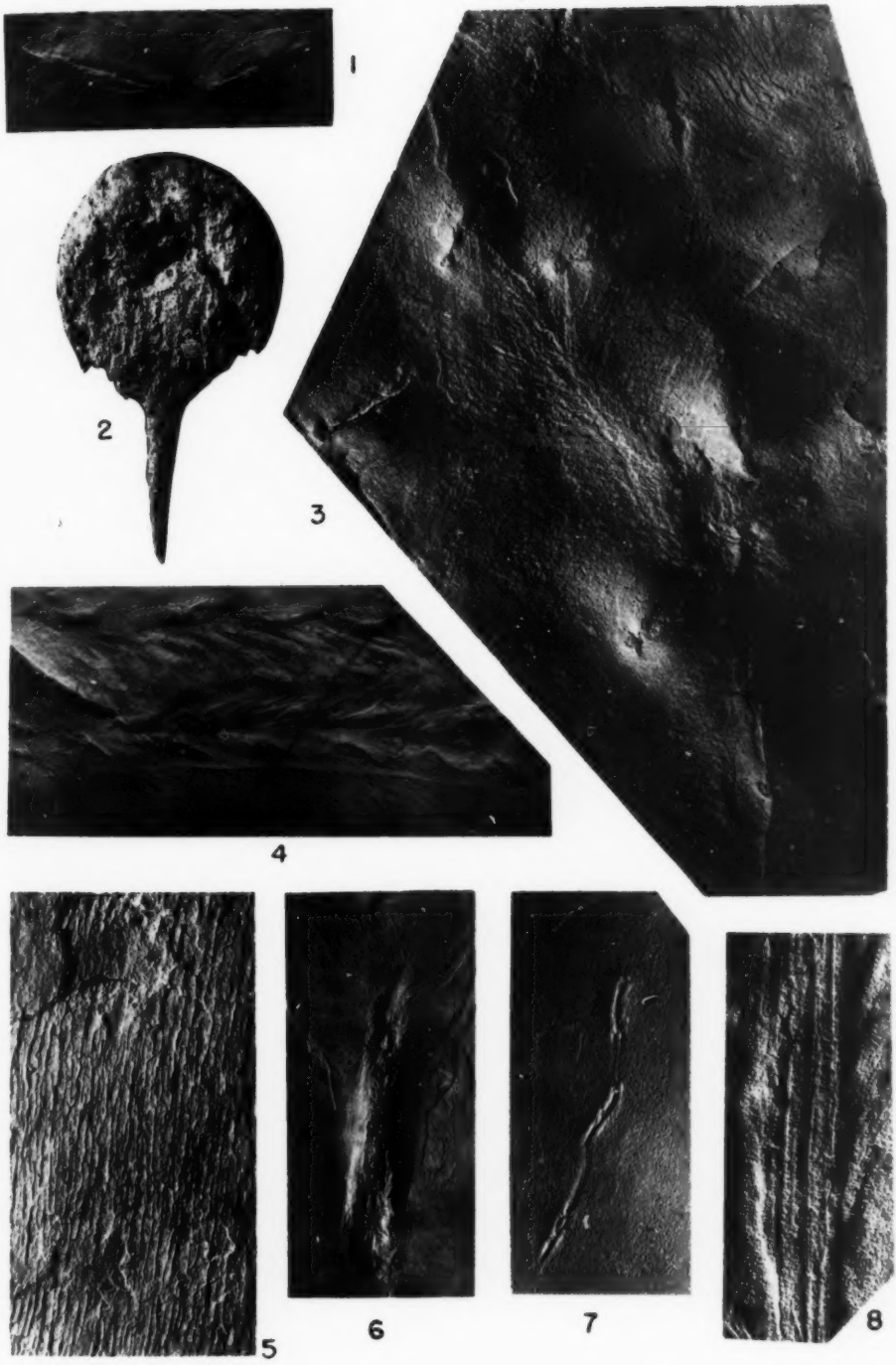
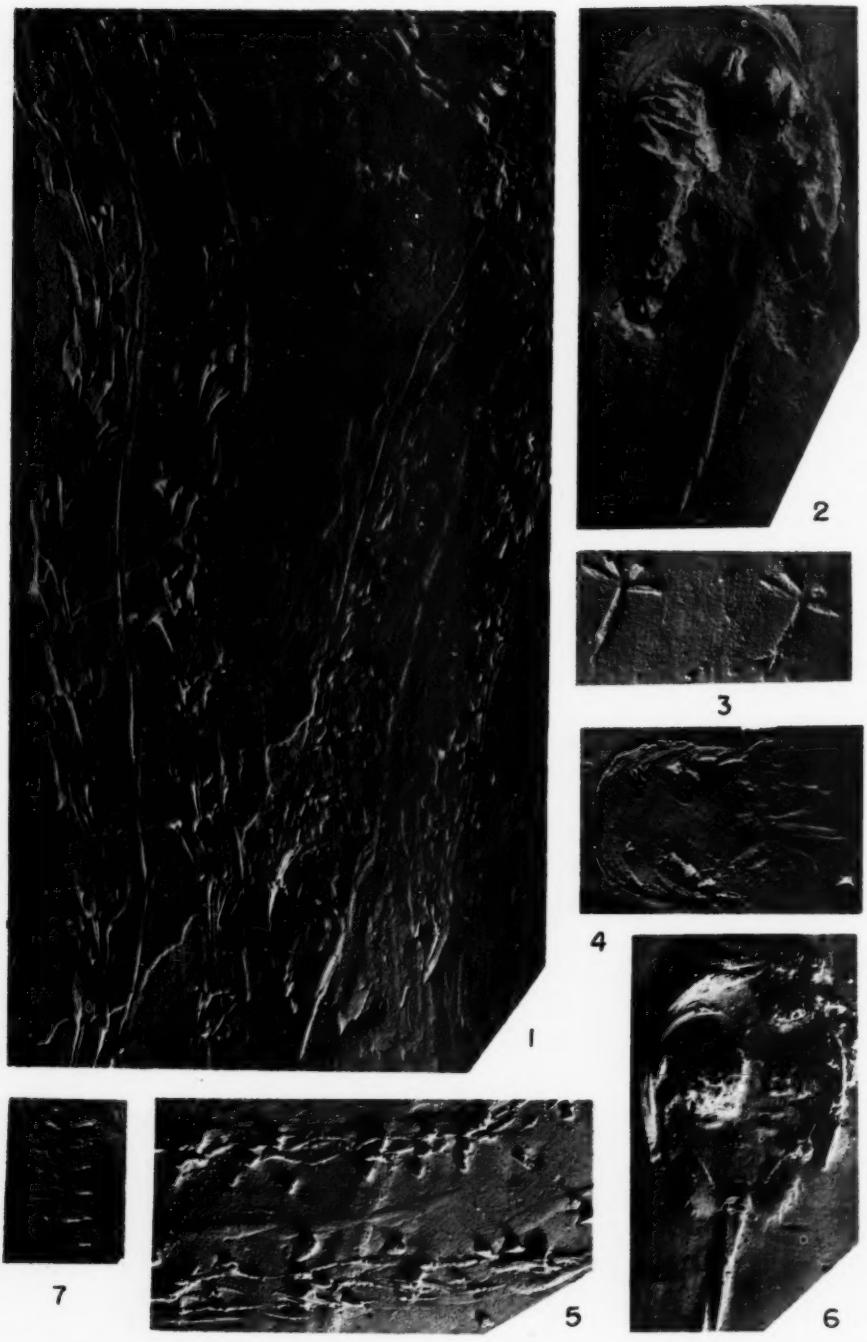
Caster, Paleozoic Tracks

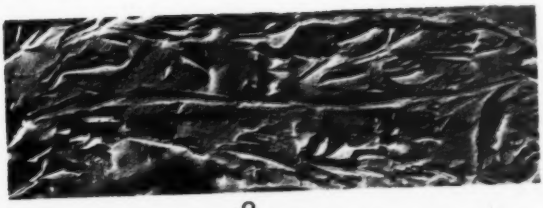


Caster, Paleozoic Tracks



Caster, Tracks of *Limulus polyphemus*

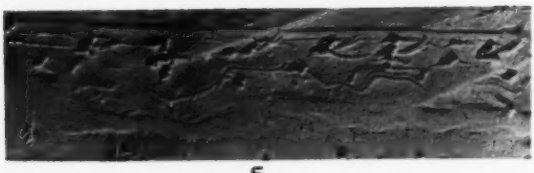
1



2

3

4



5

6

7

8

9

Caster, Tracks of *Limulus polyphemus*

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3—Trail of an immature individual illustrating (lower right) a place where the animal was temporarily stuck in the mud and later (upper middle and left) careened so far to the left that the appendages on the right side did not leave their impression. ×1.

4—Showing where a young organism stopped and presumably sank into the mud vertically and then possibly (center bottom of picture) moved off through the mud, leaving only a drag mark on the surface. The mature trail on the upper left shows some of the curious hooklike impressions seen on several of the *Paramphibius* trails. ×1.

5—Trail made by an organism pushing along with its belly in contact with the mud, thus making the peculiar drag marks here seen. The deeper parts of the resulting "chevrons" were probably made by the gnathobases. ×1.

Explanation of Plate 7

Fig. *1*—Complete trail of the *P. didactylus* s.s. type in which the molds of the simple footprints show very definite pulling of the simple feet as indicated by the long parallel grooves of the chelae and the mound of earth piled up at the proximal end of each imprint. ×1.

2—Showing the hingelike action of the outer, shorter bar of the chela of the simple foot. ×1.

3—Showing one of the anomalous groupings of simple tracks and pusher impressions that occur rather commonly in *Paramphibius* trails. When first found, and if dissociated from other more limuloid material, certainly these would pass for trails of vertebrates. ×1.

4—Showing extreme curvature of the imprint of the pusher blades. A series of such impressions in the absence of any simple tracks were interpreted (orally) as plant material when first seen. ×2.

5—Immature trail suggesting *P. didactylus* on one side and *P. tridactylus* on the other. ×1½.

6—Unusually long scratches made by the simple feet of *Paramphibius*. ×1.

7—Very characteristic trail in which chelation is obscured by the use of only half a claw for scratching and in which the pusher blades appear to be very fragile, owing to edgewise insertion in the mud. ×1.

8—Enlargement (×2) of simple impressions (molds) showing the mounds of mud at the proximal end of the chelae, which on the right side seem to be fillings of the distal articulation and on the left to be piles of mud accumulated by the foot as it was drawn back.

9—Another example of the peculiar grouping seen in *3*. Note in lower right corner the impression of the pusher and the mounds of mud at the proximal ends of the simple gashes. ×1.

Explanation of Plate 8

Fig. *1*—A series of telson impressions left by *Paramphibius* while making a turn; obviously the impressions of a rigid organ articulated at its base. ×1.

2—Circuitous trail of an immature individual, which illustrates well the reaching action of the simple feet on the outside of a curve and packing together of the footprints on the inside. ×1.

3—Mold of a series of telson impressions made on a curve where the animal was apparently partly held by the mud. Only at this point in the trail did the telson come into play. ×1.

4—A rare case where both simple feet and pushers are directed anterolaterally as though being pushed by a current or by a declivity of the mud floor. ×1.

5—Trails of the type that first suggested amphibian feet and split fin rays. ×1.

6—A series of brace-shaped incisions, which may have been made by an opercular plate repeatedly inserted in the mud; but the small size suggests quite another origin. ×1.

7—A trail of the general type shown on plate 2, figure *1*, in the same layer as that specimen. Shows clearly the interrupted impression of a tail. Made apparently on sticky mud exposed to the air. ×1.

Explanation of Plate 9

Fig. *1*—Rippled surface such as commonly underlies the more deeply impressed trails of *Paramphibius* as a subsurface deformational phenomenon. The anteriorly directed chevrons correspond to the positions of the braces of simple footprints. Note trail crossing this deformation in which tail incision is well marked. ×1.

2—From right to left across photograph is a series of scratches, which are attributed on the basis of comparison with similar scratches in the trails of *Limulus* (pl. 13, fig. *6*)

to the dragging of the abdominal peripheral spines (stylets) of *Paramphibius*. Running vertically across the photograph is a series of incisions which may have been made by the opercular plate of *Paramphibius* (compare with pl. 12, fig. *3*), and running diagonally from upper left to lower right is a series of impressions of the same kind as the vertical series, made by a somewhat larger individual, and more deeply incised. ×1.

3—Series of "inverted printers' brace" imprints, which have the same shape as the holding border of modern *Limulus* and may have been made by the serial impression of such a structure in the mud. Note that each impression is distally slightly bifid. ×1.

4—Impression of another series of "inverted printers' braces" showing the general characters of *3*, but more regularly spaced. ×1.

5—Detail of another part of the same layer as *2*, showing a smaller series of bracelike impressions that appear to have been slightly incised in the mud. ×1.

6—Serial impressions attributed to the posterolateral angle of the prosoma, right side (this being a negative of the impressions). These are judged to be imprints of the genal angle of *Paramphibius*. Presumably such a series could be made only while the animal was careening with the cephalothorax partly uplifted. ×1.

7—Trail of *Paramphibius* showing nearly continuous furrows made by the genal spines. ×1.

8—Impression of a crinoid columnal found in the midst of the *Paramphibius* trails. ×1.

Explanation of Plate 10

Fig. *1*—*Merostomichnites* sp. (cf. *Petalichnus multipartitus* Miller). Arthropod trails from the Eden shale, Cincinnati, Ohio (compare with Størmer, 1934), showing heteropody inherent in even such early trails of the Arthropoda. ×1.

2—*Asaphoidichnus* sp., showing some of the early trilobite trails to be bifid, fundamental character among the marine arthropods. From the Eden shale, Cincinnati, Ohio. ×1.

3—Showing mounds of mud, which accumulated at the proximal ends of the Ordovician arthropod tracks as in *Paramphibius*. ×1.

4—*Asaphoidichnus trifidus* Miller and smaller arthropod trails from the Eden shale, Cincinnati, Ohio. The smaller trails of the Eden show a peculiar heteropody with even suggestions of possibly pushing apparatus. ×1.

5—Larger area of the secondary trail of *Paramphibius* shown on plate 6, fig. *4*. This illustrates an unusual development of the simple hooklike impressions of the walking feet, and the not uncommon breaking down of the alignment of the simple footprints on one side. ×1.

6—Two intersecting immature trails which bear interrupted tail furrows, and illustrate the variation that the trails of two individuals show in walking over the same surface apparently at essentially the same time. Note almost complete absence of simple footprints in the trail running from left to right. ×1.

Explanation of Plate 11

Fig. *1*—Under side of a layer perforated by two dumbell-shaped incisions (Problematica). These occur abundantly in association with *Paramphibius*. ×1.

2—Natural cast of the ventral surface of *Protolimulus* sp. from the Conewango series (Salamanca suite), Asylum quarry, Warren, Pa. Collected by F. A. Randall, Pa. Second Survey collection 9635, in the Academy of Natural Sciences of Philadelphia. ×1.

3—Slab of sandy shale from the *Paramphibius* layer, which carries several of the dumbbell-shaped incisions in longitudinal series along definite lines of weakness in the layer. Note depression of upper surface of the layer. ×1.

4—*Paramphibius* trail in very wet mud showing interrupted genal spine groove on the lower side, simple chelate impressions on the outer margin of the track zone, and characteristic anteriorly directed chevrons in the middle part. Compare with plate 9, figure *7*, plate 6, figure *5*, plate 4, figure *2*. ×1.

5—Showing pattern that covers a large area of the track-bearing zone in the Lanesboro quarry, meaning not known. ×1.

6—An associated trail structure in the *Paramphibius* layer at Lanesboro. Possibly made by a burrowing pelecypod. ×1.

7—Sporadic markings of this kind in the track zone at Lanesboro may have been made by the telson touching bottom while the animal was swimming close to the mud. Modern *Limulus* frequently leaves such trails. ×1.

8—"Drag marks" ("Fucoids") associated with the *Paramphibius* trails at Lanesboro. ×1.

EXPLANATION OF PLATE 12

Trails made by immature specimens of *Limulus polyphemus*

FIG. *1*—Parts of a continuous trail made in very wet clay (the photograph is from a plaster-of-paris cast of the trail). Significant is the foot placing, drag marks made by the "cheeks" and the genal angles, the discontinuous tail impressions, which vary considerably in width and depth of impression, being a broad drag mark in the lower right and on the return from upper left to bottom is a serial drag mark made by lifting and lowering the telson, as the serial genal-spine drag marks along the edges of the left trail also show. The pushers were inserted vertically and were dragged forward through the mud as they were uplifted. Note the bifid "heel" impression. ×1.

2—A plaster cast of a "*Cruziana*-like" excavation made by a resting *Limulus* which began to sink in vertically. The pattern of the simple foot-gouges is essentially the same as in *Cruziana* (Fentons, 1937). Note also the serial record of the holding border made as the head advanced slightly during the operation. Compare with *Paramphibius* trails. ×1.

3—Plaster casts of the impressions made (artificially) by the maxillipeds (pushers) of immature limuli in soft mud. Note similarity to the pusher impressions of *Paramphibius* shown on plate 2, figures *4*, *6*. ×2.

4—Cast of the impression made by the venter of a resting crab in soft mud, which shows the chevronlike placing of the simple feet, the serial impression of the anterior margin of the prosoma, and the lashing of the telson, all of which seem to have counterparts in *Paramphibius* trails. ×1.

5—Plaster cast of a trail made by *Limulus* on rather firm clay, but with a finger being pressed slightly on the carapace to simulate an overload such as seems to have been the case with some of the *Paramphibius* trail makers. Note in lower right corner the impression of the pusher, which is used vertically in the mud. Also note the two spines of the heel. The telson drag marks give an erroneous record of the size and proportion of the tail, just as in *Paramphibius* and *Protolimulus*. ×1.

6—Cast of the impression made by a quiescent *Limulus* on soft mud. Note the "inverted printers' brace" impression of the holding border. ×1.

7—A plaster cast of a series of impressions made artificially by inserting the opercular plate of an immature dead *Limulus* in mud. Compare with plate 9, figures *2* and *5*. ×1.

EXPLANATION OF PLATE 13

Trails made by immature specimens of *Limulus polyphemus*

FIG. *1*—Plaster cast of a *Limulus* trail in rather firm mud, which shows clearly the serial nature of the genal spine furrows and the broad telson drag mark. In the upper left corner the drag marks near the middle of the trail were made by the abdominal stylets.

2—Cast of a part of a trail made by *Limulus* on soft mud. This shows very well the drag marks made by the pusher blades when uplifted and also small mounds of mud formed at the proximal ends of the simple feet.

3—Plaster cast of a trail showing hooklike gouges made by the simple feet and the parallel scratches made by the blades of the pushers.

4—Detail of a cast of a *Limulus* trail to show genal spine gouges, pusher drag, and bifid heel prints.

5—Detail of plaster cast of young *Limulus* trail, which shows the impression of the chelae of the simple feet and the superimposed imprints of the pushers. The drag mark in the middle of the print was formed by fecal matter which trailed behind the moving crab.

6—Detail of a plaster cast to show usual drag marks made by the abdominal spines (stylets) when the animal careened or rounded a curve too rapidly.

7—Cast of a trail made on very stiff mud. Note absence of telson mark. The tail was held upright the entire time of this experiment. Note the presence of both the impression of the "sleigh-runner" edge of the cephalothorax and the genal spines in series. The animal walked on the tips of the simple feet and the ends of the pusher blades, thus making only commalike pricks on the mud.

8—Detail of trail made by a crab on mud, which was a little more plastic than in *7*. Note dragging of the telson, sleigh-runner and genal grooves, and deeper impression of the feet.

9—Trail on mud of the plasticity that seems closest to the condition in *Paramphibius* trails. Made by the same individual as *8*.

The anatomy of *L. walchi* was very close to that of modern *Limulus polyphemus* (Walther, 1904), and the track record is similar in every respect. In none of the extant tracks or illustrations, however, are the pusher impressions clearly shown. This is especially amazing when it is recalled that the Solnhofen record is of death-struggles and every trail, when followed to its end, is terminated by a dead crab (Walther, 1904). Certainly in such an environment, when every ounce of energy was being expended (Abel, 1935) the pushers must have been employed and ought to have left a record! This illustrates well the fortuitous circumstances that surrounded the Devonian organisms at Lanesboro when such an abundant record of pushers was left. These Jurassic records also make it seem more plausible to attribute the simple *Merostomichnites* trails to *Protolimulus* and to interpret them as essentially the same thing as *Paramphibius*. The simple footprints of *L. walchi* agree in every respect with those of *Paramphibius* except size. Jurassic and modern Xiphosura grew larger than Devonian forms. The telson impressions of the Jurassic crabs are almost exactly like those of *Paramphibius* and *Merostomichnites*, as are also the ventral "chevron" markings made by the gnathobases and gill books and the lateral drag marks made by the abdominal stylets.

This comparison of the trails of *Paramphibius* with those of the pretty clearly established (*Merostomichnites*), inferred (*Paleolimulus*), or clearly demonstrable (*Limulus*) trails of the Xiphosura Limulida (classification outlined by Størmer, 1934) brings out rather forcibly the necessary assignment of *Paramphibius*, but before drawing final conclusions, let us compare the inferred structures of the maker of the *Paramphibius* trails with the structures of the Xiphosura Limulida in the late Paleozoic.

COMPARATIVE PALEOMORPHOLOGY

How does the inferred anatomy of the *Paramphibius* trail maker compare with that of the American representatives of the Xiphosura Limulida in the late Paleozoic? For the purposes of this paper it seems sufficient to outline structural comparisons between *Paramphibius* and the two described representatives of the family Limulidae that are reported from the American Devonian: *Protolimulus* Packard, 1886, and *Paleolimulus* Dunbar, 1923. The family Limulidae as here used does not include *Euproops* Meek or *Prestwichianella* Woodward, for which it seems advisable that a separate family be erected. Packard (1885) assigned these genera to the Belinuridae. They have received additional attention by Kobayashi (1933) and Størmer (1934). *Kieria*, which Størmer included temporarily in the Limulidae, is also omitted from consideration here. It is impossible, however, from the information to be gleaned from the trails and tracks of *Paramphibius*, definitely to disprove relation-

ship with the Carboniferous genera *Belinurus* Konig and *Prestwichianella* Woodward. Eller (personal communication, 1936–37 and demonstration at Geological Society meetings, Cincinnati, 1936) has in process of description two new specimens of Limulida from the Upper Devonian of Pennsylvania. One specimen comes from the Conewango series and may be conspecific with *Paleolimulus? randalli* (Beecher), Dunbar, 1923, from the same locality and series. The other specimen comes from a lower horizon (see fig. 9). Eller reports that this latter specimen shows affinities with the Carboniferous genus *Prestwichia* (*Prestwichianella*), but after casual examination it seemed to the writer referable to a new genus in the Limulidae. When Eller's paper appears, his conclusions will undoubtedly have considerable bearing on the interpretation of *Paramphibius* and *Merostomichnites beecheri* and will undoubtedly clarify the relationships of *Protolimulus* and the Devonian forms referred to *Paleolimulus*.

Figure 9 shows the relative stratigraphic positions in the Upper Devonian of the representatives of the Limulida mentioned above. The stratigraphic details of the area have been taken up rather fully by Butts (1908), Caster (1934), and others, and are summarized in this paper. It will be seen that *Paramphibius* occurs farthest east and at the lowest horizon of all (fig. 9, locality 1). Eller's "*Prestwichia*" (personal communication, 1936–37) comes from the Conneaut shale ("Chemung") near Wellsville, N. Y. (Chadwick, G. H., *fide*, Eller, E. R., letter, Jan. 1937; and Woodruff, J. G., manuscript report on the Wellsville quadrangle, N. Y., letter, Feb., 1937), in association with the famous dictyosponges (Hall and Clarke, 1898, Eller, 1935) of the Conneaut. *Protolimulus eriensis* and *Paleolimulus? randalli* come from the Conewango (i.e. uppermost Devonian) series of northwestern Pennsylvania.

The newly discovered Xiphosuran from the Conneaut is known only from a well-preserved carapace, which has the general proportions of the Carboniferous genus *Prestwichianella* (*Prestwichia* is preoccupied, Størmer, 1934). It possesses posterolateral prosomal extensions, a broad, anteriorly rounded prosoma, and partly fused buckler. Its carapace characteristics are such that it would most certainly make a *Paramphibius*-like trail if endowed with limuloid appendages. No merostomaceous trails have yet been described from the Conneaut shale, however.

The Conewango series has yielded most of the American Devonian representatives of Limulida. First described, and most abundant of these fossils is the form known as *Protolimulus eriensis* (Williams) Packard, 1886, (*Prestwichia eriensis* Williams, 1885). The original specimen was redescribed and redrawn by Hall (1888), and an additional specimen was illustrated by Caster (1930). All known representatives occur in the form of ventral casts of the organism.

On plate 11, figure 2, of this paper a new specimen of *Protolimulus* is also illustrated from the middle Conewango series. This specimen was found in the Pennsylvania Second Geological Survey Collection (no. 9635) in the Academy of Natural Sciences of Philadelphia. In the Catalogue of the Survey Collection (Randall, 1889) it was listed as a "fucoid" from the Tanners Hill quarry at Warren, Pa. (middle Conewango = Salamanca suite). Incidentally this specimen was probably the first ever found of the form that Williams (1885), described as *Prestwichia eriensis*, for the work on Warren County, Pa., and the Oil Region was completed by 1883 when the Warren County Report (Carll, 1883) was published. Williams' specimen from the basal Conewango (LeBoeuf sandstone = Panama conglomerate) was collected in 1884 or 1885 by C. S. Prosser (personal communication of G. D. Harris, 1935, who was a student of Williams and Prosser at Cornell University at the time). Other specimens have been found by the author in various localities in northwestern Pennsylvania and at various horizons in the Conewango series.

Chief of these discoveries were those mentioned above, which occur in association with *Merostomichnites* or *Paramphibius* trails and tracks from the middle Conewango near Ridgway, Pa. (fig. 8, no. 4), and in the uppermost part of the Conewango series on the Chestnut Ridge anticlinal inlier in the southwestern part of Pennsylvania (Caster, Torrey and Chadwick, 1935; Willard and Caster, 1935) (fig. 8, no. 10).

The genal spines of *Protolimulus* scarcely protruded to interrupt the regularity of the outline of a distinctly circular anterior margin. This fits the general picture of the spine and "sleigh-runner" impressions inferred for *Paramphibius*. That the buckler was more anchylosed than Williams originally supposed seems obvious from the parallel lines that Williams interpreted as adventitious carinae of the buckler in his figure 2, and which consistently, but of varying length, characterize the casts of the venter of all known protolimuli. It would appear that there is a definite connection between the peripheral spines of the buckler and these longitudinal gouges in the mud wherein *Protolimulus* rested. That these parallel carinae in the casts are the filling of gougings made by the "abdominal" spines during the inflection of the buckler against the cephalothorax is suggested from the observation of similar marks made by the buckler spines of modern *Limulus* when resting in the mud and occasionally folding up and unfolding without making any forward progress. Additional specimens tend to prove that these buckler spines were not nearly as blunt as Williams indicates in his dorsal reconstruction; and if the inflection action is properly deduced, then too the broad base of the tail of Williams' specimen is explained, for both were *worn* grooves, the fillings of which would give a

distorted picture of the actual shape and size of the abrading organs. The abdominal spines of *Protolimulus* were probably sharp and quite capable of making the same type of scratches as are recorded (pl. 9, figs. 2, 5) by the *Paramphibius* trails. Likewise the telson of *Protolimulus* was probably not as broad basally and not as stubby as Williams and Hall thought and could have easily made telson markings such as are seen in *Paramphibius*. The Philadelphia Academy's specimen of *Protolimulus* (pl. 11, fig. 2) was a "thin-tailed" form and would tend to support this contention.

Hall and Williams concur in interpreting certain striations just inside the impressions of the genal spines in the holotype of *Protolimulus* as probably impressions of "the foliatious terminations (?) of the last pair of limbs" (pushers). Of considerable importance, it would appear, in interpreting the impressions in *Paramphibius* that are attributed provisionally to the operculum is the cast of a structure in *Protolimulus* described by Hall as follows:

> Behind these appendages (pushers) and situated at about the center of the surface of the fossil, is a transversely elongate, triangular impression (apex anterior) having the position of the thoracic or opercular plate in *Limulus* and the Eurypterida. The apex of this impression lies in the axial line, its lateral slopes are long, and its length is less than one-half its width along the posterior margin. Two parallel longitudinal furrows divide it into a median and lateral area, and these furrows appear to be carried for considerable distance posteriorly over an area that may have been the continuation of this plate. Admitting that it was thus produced, there is evidence that it was divided by a transverse furrow or suture, making the analogy of its structure with that of the thoracic plate (operculum) of *Limulus* very striking.

Such an organ would be able almost perfectly to make ovipositor slits of the type seen so commonly associated with *Paramphibius*, as shown on plate 8, figure 6.

In his original specimen of *Protolimulus*, Williams thought that there was evidence of a hypostomal plate, but subsequent specimens have failed to show this impression, and it seems wise to accept Hall's interpretation at least for the present. Williams described the plate as follows:

> The infolded frontal border is broad and convex anteriorly, narrowing to the base of the genal spines. In the axial line its edge, or a ridge upon its surface, appears to be connected with a bisymmetrical trifoliate plate, which lies in front of the probable position of the mouth and extends backward, its largest lobe lying in the axis.

However, Hall suggests the apparently more plausible explanation of a *Limulus*-like holding edge, of which the hypostomal platelike area is merely the most posteriorward extension, as in *Limulus*. The apparent sutures of the plate are just as probably accidental groovings in the mud bed. For, says Hall:

> Such an interpretation of the character is not unsupported by the appearance of the fossil and obviates the necessity of supposing the animal to have differed from the Limulidae in the possession of a hypostome, while agreeing in other respects.

If Hall's interpretation is correct, it is probable that *Protolimulus* could

have made serial "holding-carina" impressions comparable to the occasional bracelike marks found on the trails of *Paramphibius*.

An imperfect prosomal carapace from the middle Conewango was described by Beecher (1902) as *Prestwichia randalli* and later referred with doubt to the genus *Paleolimulus* by Dunbar (1923) when he described the unusual new genus and species, *Paleolimulus avitus* from the Permian insect beds of Kansas. Beecher's incomplete specimen is hardly sufficient for generic determination in a group that so largely depends on the character of the buckler or abdominal segments. Dunbar's determination of the incomplete specimen is as satisfactory as any could be until more material is found. Assuming that the determination is accurate, it is interesting to compare the inferred characters of the *Paramphibius* trail maker with *Paleolimulus avitus*, the genotype of *Paleolimulus* from the Permian. First, it is not impossible that *Paleolimulus? randalli* and *Protolimulus eriensis* are congeneric, if not conspecific. However, *P. randalli* has a shorter and more transverse cephalic shield than the *Protolimulus* casts. Inasmuch as the dorsal prosomal characteristics of *Protolimulus* are unknown, the comparison cannot be carried further. As a matter of fact, the general shape of the head shield of *Paleolimulus* s.s. agrees more nearly with *Protolimulus* than it does with *P. randalli*.

It was probably an animal of the *Protolimulus-Paleolimulus* stamp that made the original *Paramphibius* trails and the younger Devonian *Merostomichnites* trails. In *Paleolimulus* the body is characterized by an enormous cephalothorax of subequal length and breadth (genotype) and a relatively smaller buckler (width of cephalothorax at genal spines 1.5 mm.; greatest width of buckler 0.875 mm.; length of buckler 0.75 mm.). Telson and buckler are subequal in length. The genal spines of *Paleolimulus* were slightly extended posterolaterally as, it would appear, the spines making the outside grooves of *Paramphibius* trails must have been. The buckler carried marginal movable spines (stylets) such as leave their impression in the trails of *Paramphibius* (pl. 9, figs. 2, 5). Fortunately the prosomal appendages are preserved on the type specimen. They appear to have been almost precisely the same as those postulated for the *Paramphibius* trailmaker. Four pairs of simple chelate walking legs, weak and dangling (at least not shown) antennules, and strong maxillipeds, which were either terminated by four sharp (?) spines, the posteriormost of which was the longest (Dunbar, 1923), or having three (or more?) spines at the distal end of the propodos and a backward bent dactylus (Dunbar, personal communication, May, 1937). The latter condition seems more likely and is in general the condition postulated for *Paramphibius*. The actual number of pusher blades in the Kansas specimen is uncertain, as is also the general nature of the longer

spines or dactylus. Proximal portions of the walking legs appear as indistinct anteriorly directed (and incomplete) chevrons along the mesial line of the prosoma, in the position postulated for the bases of the coxae (coxagnaths) in *Paramphibius*. It seems likely that *P. randalli* shared these general characteristics with *P. avitus* and may, therefore, next to the casts of *Protolimulus*, give us our best information on the organization of Devonian representatives of the Limulidae. The specimen of Limulida that Eller (Geological Society meetings, Cincinnati, 1936) is describing from the Conewango series at Warren, Pa. (fig. 9, no. 6), may belong to the same stock as *P. randalli*, and in proportion is not more dissimilar than are the other recognized specimens of *Paleolimulus*.

It seems likely that the ancestral stock of the Xiphosura Limulida was the Xiphosura Synziphosura by way of the family Weinbergerinidae as Richter and Richter (1929, p. 205) have maintained. This monotypical family (*Weinbergerina opitzi* Richter and Richter) seems to have been characterized by five pairs of prosomal appendages, which bore at least two penultimate movable spines in essentially the same position as the pusher whorl in *Limulus*. Moreover, in *Weinbergina* of the Hunsrückschiefer all appendages bear terminal movable spines, which are very similar to those that are found on the pusher legs of *Paramphibius* and *Limulus*. It seems not impossible that the pusher-legs of *Paramphibius* and modern *Limulus* may hark back to the synziphosurous condition of all appendages, whereas the normal walking legs of the Xiphosura Limulida from *Paramphibius* to the modern king crabs have developed along quite different lines so that little of the synziphosurous condition is reflected in their organization. It seems unlikely, as the Richters state, that the terminal chelae or hooks of the limuloid walking legs were derived from terminal spines in the Synziphosura.

Part II. Additional Geological and Biological Considerations

Both comparative ichnology and comparative paleomorphology have shown us the abounding likelihood of *Paramphibius* trails being of limuloid origin and of the trail maker having been an ancestral king crab. Plausibility is added to this conclusion by the relatively abundant occurrence of representatives of the Limulida in the Upper Devonian, albeit at a little higher horizon than *Paramphibius*. The amazing similarity between the trails of *Paramphibius* and modern *Limulus*, which, unsupported by additional data, might be dismissed as a fortuitous coincidence, becomes a cogent argument in the light of this additional evidence. That the Xiphosura are a more or less long-standardized stock has been long appreciated by zoologists. Henry Woodward wrote (Geol. Soc. London, Quart. Jour., vol. 23, p. 35, 1867) of the Xiphosura:

> Few orders can be compared to the Xiphosura for persistency. . . . Had *Limulus* represented a higher type of articulation it is hardly conceivable that it could have existed so long, and apparently unchanged. But it seems to have been one of those eccentric groups that appear from time to time in the zoological series, which, branching out into a by-way of its own, is checked from further onward progress; but being possessed of tenacity of life and great power of reproduction, it holds its ground whilst higher orders have been modified or swept away.

Thus far the strictly paleontological aspects of *Paramphibius* have occupied our attention. It is now proposed to examine the stratigraphy of the Upper Devonian and the "facieology"[3] of the Catskill delta in so far as it applies to the current problem and correlate if possible the occurrence of *Paramphibius* at Lanesboro with the other known Xiphosura trails or remains that have already been discussed.

OCCURRENCE

The type locality for *Paramphibius* trails is Lanesboro, Susquehanna County, Pa. (Susquehanna topographic sheet). The type trails are known only from a narrow shale band near the middle of a shale overburden in a sandstone (flagstone) quarry high on the hill on the south side of Starruca Creek, about 1½ miles east of Lanesboro. The precise locality was indicated by Willard (1935), and the general locality is shown on the accompanying diagram (fig. 6, no. 1). The mountain road to the quarry is easily discernible at all times from the State highway a short distance east of the grade crossing in Lanesboro. The quarry itself can be seen from this point in the fall or winter. The quarry is reached most easily by following the Erie Railroad tracks on the south side of the creek to the first log road up the mountain (hill) southeastward. Willard gives the elevation of the quarry as 1,200 feet above sea level, which is about 300 feet above the Susquehanna River at normal stage at Lanesboro.

The localities at which *Paramphibius*-like trails and tracks have been obtained in northwestern Pennsylvania and southeastern New York have been indicated at their first mention in the preceding text. These localities are also shown on figure 6.

Paramphibius trails occur in the lower middle part of the Upper Devonian rocks of Pennsylvania (Chemung stage of the Chautauquan series). Also during the summer of 1937 Dr. G. R. Megathlin of the Geneseo State Normal School, New York, collected several specimens of *Paramphibius* trails from a 10-foot layer of fissile red shale lying between two gray-green shale zones in the "Catskill" strata 9 miles east of Hancock, N. Y., on Route 17 (N. Y. and U. S.); the trails and tracks are so similar to those from Lanesboro that there can be no question of their identity. The horizon is essentially the same as that at Lanesboro, in a more shoreward facies.

[3] "Facieology" and "facieological" would be very convenient terms for the geologist, paleontologist, and paleoëcologist in dealing with facies matters, which play an ever increasing rôle in all phases of geology and biogeology.

Merostomichnites trails and *Paramphibius*-like trails have been found by the writer in the upper part of the Upper Devonian (Conewango series). The remains of limuloid crabs are known from the upper middle part of the Upper Devonian (Conneaut stage of the Chautauquan series). This stratigraphic relationship is brought out by figures 7 and 9.

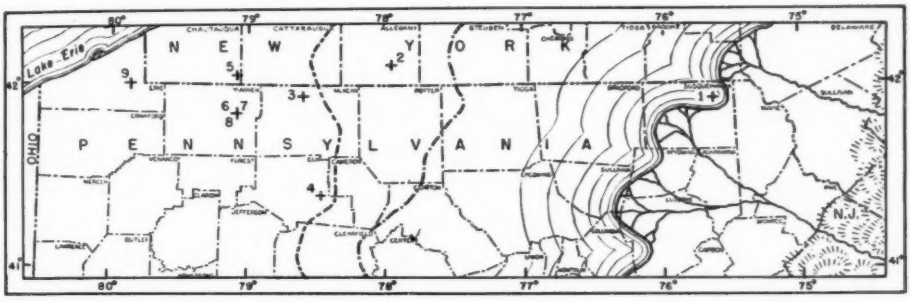

FIG. 6.—Northern Pennsylvania and adjacent portion of New York showing the geographic distribution of the Upper Devonian Xiphosura: 1. Lanesboro, Pa.; 2. Wellsville, N. Y.; 3. Lewis Run, Pa.; 4. Ridgway, Pa.; 5. Pope Hollow, N. Y.; 6, 7, 8. Warren, Pa.; 9. Le-Boeuf, Pa.; 10. not shown on map, on the northwest flank of the Chestnut Ridge anticlinal inlier near Uniontown, Pa. Hypothetical shore lines at three stages of the Upper Devonian indicated. Solid line—late Cayuta or early Wellsburg time; dash-dot line—late Canadaway or early Conneaut time; long and short dash line—early Conewango time, which was about the line of maximum westward advance of the shore. The Conneaut and Conewango shore lines may have tended more southwesterly than here indicated. The Chemung shore line is modified from Willard, 1934.

Recently the stratigraphy of the Upper Devonian strata that were deposited in New York and Pennsylvania during the accumulation of the Catskill and other delta deposits (Barrell, 1914) has been considerably revised, chiefly through the works of Chadwick, Willard, Caster, and others. They have emphasized the fact that had been suspected or known for a long time (Williams, 1913) that the earlier stratigraphers had correlated their strata along the east-west line of outcrop in this area principally on lithologic similarity or general faunal content. The result was a misinterpretation of lithic units for coeval time units, of facies bands (magnafacies) for stratigraphic units (formations). This relation is brought out by figure 9. The current clarification, while shedding much light on natural relationships, has necessarily, and quite unavoidably, resulted in some nomenclatorial confusion through the piling up of synonyms. In the following discussion of stratigraphy and facieology, this condition must be borne in mind.

The general relation of facies to time lines in eastern Pennsylvania is shown by figure 9. In this figure the meridians are indicated at the top. The time lines (contemporaneity lines, Caster, 1934) are seen to cut across the facies boundaries (facies

planes, Caster, 1934), which advance westward (and upward in the rock column) as time progresses (in normal off-lap or regressive over-lap condition). Six belts of different facies (environments of sedimentation and life, or *magnafacies*, Caster, 1934) run roughly parallel. Four of these magnafacies are of marine origin and lie west of the shore (roughly shown by the stippling between the Catskill and Big Bend zones). Two terrestrial magnafacies are shown east of the shore line (a portion of an even more eastern magnafacies is shown on fig. 7). From land seaward the six magnafacies have been given names as follows: Tioga, Catskill, Smethport, Big Bend, Chagrin and Cleveland. These have been discussed in some detail by Caster (1934). Their differentiation has been based on lithology and ecological assemblages of fossils.

The time lines (lines of contemporaneity) divide the sediments into series, stages and monothems, as shown by the diagram and by Caster (1934). The series and stages of the Upper Devonian are as follows (youngest on top):

Conewango series
  Riceville stage
  Venango stage
Chautauquan series
  Conneaut stage
  Canadaway stage
  Chemung stage
Senecan series

The Chemung stage is subdivided into two monothems ("formations"), the Cayuta (older) and Wellsburg. *Paramphibius* trails at Lanesboro occur in the lower part of the Wellsburg monothem in a member known as the Kingsley shale.

The rocks dip slightly to the southwest (initial dip plus subsequent slight tilting), i.e., the time planes are not horizontal and the facies planes have been brought to a position of essential horizontality. Limited outcrop obscures this point, and earlier geologists consistently mistook the facies planes for time planes in making regional correlation. The rectifying of this misconstruction of long-standing has brought about the present multiplicity of synonyms for rock (time) units (see Chadwick, 1933, 1935). For example, in earlier reports, wherever in this area a sequence of clastic marine strata that carries a marine fauna is overlain by red beds (Catskill) of continental origin from the eastern part of New York and Pennsylvania into Ohio, the marine beds were called "Chemung." But when the sequence occurring along the meridian of 76°, which is essentially the type area for the Chemung, is studied and plotted, it is found that this formation underlies by many feet the similarly appearing strata immediately underlying the red beds westward, e.g., between 78° and 79° in western New York and Pennsylvania. The term Chemung, which was originally used in a stratigraphic sense for a definite section of rocks, representing a precise time unit, had been subsequently applied inadvertently in a facieological sense, thus giving several "Che-

mung" homonyms for strata younger than the true Chemung.

The section of the strata at Lanesboro brings out the stratigraphic position of *Paramphibius* in eastern Pennsylvania. The bearing of this sequence to the lithic sequence shoreward in eastern Pennsylvania and seaward in western Pennsylvania, where other xiphosuran evidence is recorded, is shown in figure 7. The section also brings out some of the lithologic and faunal data on which the following conclusions as to facies have been reached.

The following section of the rocks exposed in the vicinity of Lanesboro, Pa., is taken from the published reports of White (1881), Willard (1934–36), and field studies by the writer (1935–36). Both Willard and the writer were materially assisted in the field by Mr. D. H. Harding, a local geologist of Susquehanna, Pa., who has long studied the local geology and who first discovered *Paramphibius* trails more than 20 years ago (Harding, personal communication, 1935).

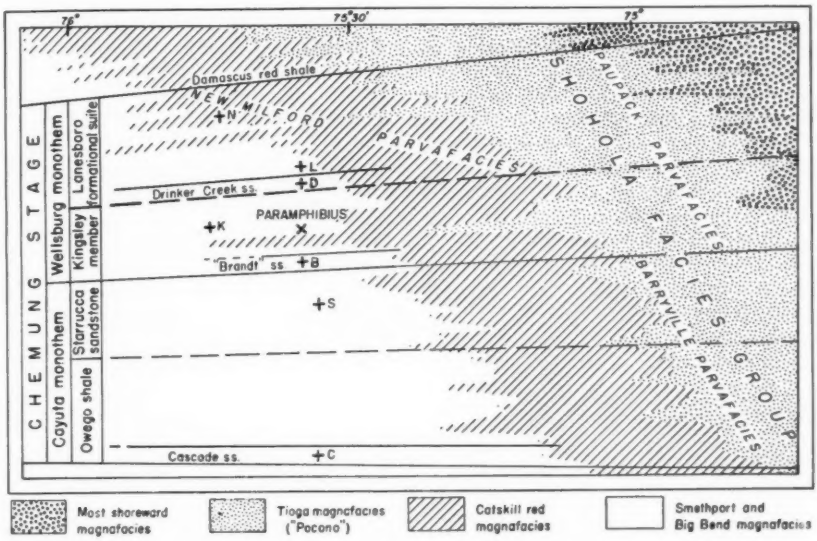

FIG. 7.—Summary of the stratigraphy and the stratigraphical and facieological nomenclature of the Chemung stage of the Upper Devonian in northeastern Pennsylvania. The generalized cross section runs essentially east and west and is at approximately a right angle to the progressively westwardly advancing Upper Devonian shore line in the Penn-York embayment. Digitation of facies boundaries is largely generalized east of 75°30′. Meridional position of the geographic features used in naming the stratigraphic units at Lanesboro are indicated by crosses and initial letters, i.e., L—Lanesboro, N—New Milford, etc. The position of the crosses within the units have no stratigraphic significance. Horizon of *Paramphibius* indicated by "X". The most shoreward magnafacies, which is indicated in the upper right corner of the diagram, is known in this region only by occasional coarse conglomeratic lenses, which enter the "Tioga" magnafacies from the east and southeast.

COMPOSITE SECTION OF THE UPPER DEVONIAN STRATA NEAR LANESBORO, PA.

Chautauquan series. According to Chadwick, 1935, the fauna of the Chemung represents the last stage of the Senecan series rather than the first of the Chautauquan. Although the matter is largely one of degree, Chadwick does make a strong case for his thesis.

Chemung stage (=principally the Shohola formation, Willard, 1936, pp. 585–586)

A. Wellsburg (Williams and others, 1909, p. 76) monothem [=Päupack formation, (White, 1881, pp. 59, 68; emend. Willard, 1936, p. 586); parts of New Milford group (White, 1881, pp. 68, 92); New Milford formation (Willard, 1936, p. 586).]

1. Lanesboro formational suite (term: Caster, 1934, p. 18) [=member (Willard, 1936, 586); New Milford upper, middle, and lower sandstone (White, 1881, p. 70)] Greenish to grayish flags and sandstones, which are markedly lenticular as individual units, but remarkably persistent as a suite. The sandstones are generally cross bedded. Typically the suite consists of a massive sandstone or flaggy zone at the top, a predominantly shaly zone in the middle, and a prominent sandstone zone at the base. The suite is sparsely fossiliferous in the lower two-thirds with marine fossils and triturated plant material. Occasional red or pinkish layers are locally present.....about 350–400 feet.
   a. Drinker Creek sandstone member (new name, this report) [=New Milford lower sandstone (White, 1881, p. 69)] Micaceous, quartzose sandstone which is usually gray or olive greenish in color; grain size varying from fine sand to thin layers of flat vein-quartz pebbles of as much as 1 inch in diameter. Whole layer more or less lenticular and locally broken into flags and shales and therefore almost unrecognizable. Marine fauna relatively abundant in local occurrences (see discussion, below) and usually associated with considerable triturated wood.....about 25 feet

2. Kingsley member (Willard, 1936, p. 589) (=New Milford red shale, White, 1881, p. 68, 70, and taken to be the real definition; and only the upper half of the same, White, 1881, p. 77, diagram; draughtsman included Kingsley shale with the New Milford red shale of p. 68 and 70 by an erroneous bracket.)
   a. Strata in contact with the Drinker Creek sandstone not known, but from talus inferred to consist of olivaceous shales and gray sandstones containing a sparse marine fauna; possibly a thin layer of red shale.....about 25 feet
   b. Alternating layers of grayish to olivaceous shale and flagstone; shale predominating; marine fauna relatively abundant in local "pockets" of the shale; less common in the sandstone, except in occasional sandy shell breccias an inch or so in thickness.....about 25 feet
   c. Fine-grained olive shale and mudstone with very thin layers of undulating sandstone and occasional layers of flagstone as much as 1½ inches in thickness. Marine fauna sparse throughout. (Top of track quarry.).....6 feet
   d. *Paramphibius* shale in the Lanesboro quarry. Characterized by olive color, even texture, smooth even bedding, fine grain and micaceous silty composition. Shale alternates with ¼- to ½-inch layers of undulatory sandstone marked with worm burrows and tracks. The tracks of *Paramphibius* occur at two horizons about 2½ feet apart, about 1 foot from the top of the unit....5 feet
   e. Shale and thin layers of sandstone in alternation, not dissimilar in general characteristics to shale above the track zone, but carrying a more abundant marine fauna. Flags more abundant in lower part, where they apparently grade into the main flagstone quarried where *Paramphibius* was found..15 feet
   f. Somewhat massive sandstone, which splits along low-angled cross-bedding diastems and shale partings into commercial flagstones. Marine fauna throughout, but very abundant in certain shell layers. This sandstone is much quar-

ried in the Susquehanna area, and is known locally as the "Brandt." sandstone. It was the reason for the opening of the *Paramphibius* quarry originally. About 30 feet

B. Cayuta (Williams, 1907, p. 75) monothem [=essentially the Barryville formation (Willard, 1936, p. 586); in part (erroneously?) New Milford red shale (White, 1881, p. 77)]

3. *Starruca shale member* (White, 1881, p. 75) [=? essentially the Swartwood member and Third Tropidoleptus zone (Williams, 1906, vol. 14, p. 580; vol. 15, pp. 97, 108, 109; 1913, p. 7), (erroneously?) basal 105 feet of New Milford red shale (White, 1881, p. 77); basal 105 feet of Willard's Kingsley shale, 1936, by inference]. Olivaceous, more or less fissile shale that carries thin, but seldom prominent sandy lenses. Fossiliferous throughout, but with great numbers of fossils in basal fourth. Usual expression is a long gentle talus slope with more or less steep declivity near base where limy fossil horizons became abundant. Considered as top of the Chemung by I. C. White (1881, pp. 97, 98, but not so considered, p. 77) .... about 125 feet
4. Owego (Williams, 1906, pp. 580, 108, 109, 97) shale member (bearing the second *Tropidoleptus* zone of Williams, 1906, 1913, to the west; considered (erroneously?) top of Chemung by White, 1881, p. 77).
   a. Olive to gray sandstone carrying some flat pebbles near the middle, which is locally a true conglomerate layer as much as a foot thick; marine fossils, triturated wood, and local coquinite layers.....about 10 feet
   b. Olivaceous shale, somewhat reminiscent of the *Paramphibius* shale of the Lanesboro quarry; thin sandstone layers; marine fauna sparse.....10 feet
   c. Olive shale and gray flaggy sandstone, both of which carry an abundant marine fauna and occasional coquinite layers. Near the middle are at least two reddish zones ("iron ore") which locally carry some pyrite in nodular form; occasionally, usually on weathered surfaces or where ground water has penetrated, limonite is plentiful in these red zones.....about 42 feet
   d. Tongue of bright ("brick") red shale, which is fissile and readily disintegrated, thus occasionally giving the impression in the color of the soil or talus of a much more extensive red zone. A very persistent datum in the Susquehanna area. No fossils noted.....about 10 feet
   e. Olive and gray shales and sandstones in alternating sequence. The flags are sometimes locally thickened sufficiently and replace the shale so as to form a prominent bench. Occasional reddish or purple shale indicated by soil and talus coloration. Marine fauna throughout.....about 40 feet
5. Cascade Creek sandstone (White, 1881, pp. 74, 75) member (Willard, 1933, p. 506; 1936, pp. 31–32). Usually massive, coarse gray to olive-green sandstone; highly micaceous, and usually stained with iron oxide. Made up of several lenses which are not individually traceable over a great distance, yet the unit as a whole is very persistent. Layers of coarser flat pebbles and even conglomeratic layers are locally developed; an abundant marine fauna usually present and everywhere associated with an abundance of triturated plant material. Locally contains considerable lime, apparently derived from included shells.....25–30 feet

Shales and sandstones referred to the Enfield stage.

The details of the correlations indicated in the above section are shown on figure 7.

The name *Drinker Creek sandstone* is here proposed for the basal unit of the upper sandstone sequence of I C. White's New Milford group (i.e., New Milford lower sandstone), which crops out generally in the Susquehanna and Lanesboro area of Susque-

hanna County, Pennsylvania, as well as more widely. The lithic characters of this member are summarized in the above section. The Drinker Creek sandstone has been studied in considerable detail by D. S. Harding of Susquehanna. It is well exposed in old quarry pits near the forks of Drinker Creek about 1½ miles south of Susquehanna, which is taken as the type locality. Figure 8 is a photograph of this exposure. White and others considered the entire New Milford group to be barren of fossils, but Harding has found characteristic marine faunas in the lower half or more of the Lanesboro suite. The biota of the Drinker Creek sandstone, which Willard records from Harding's collections, augmented slightly by a study of a large collection of these fossils which Mr. Harding gave to the writer in 1935 follows. Mr. Harding informs me that the fossils, which he collected near the forks of Drinker Creek, came from

FIG. 8.—Type area for the Drinker Creek sandstone of this paper. The encircled spot in the distance upper left is the quarry in this member from which Mr. Harding collected a large marine fauna. Along the road below the Drinker Creek exposure in the quarry is exposed the "Brandt" sandstone, which underlies the *Paramphibius* zone by about 15 feet. This picture well illustrates the typical scenery of Susquehanna County, Pennsylvania, with its rolling terrain, drift-covered hills, and few outcrops. Photograph by D. S. Harding.

the New Milford lower sandstone (Drinker Creek) and not the unit "4-c" of the above section, as has been recorded (Willard, B., 1935 p. 45).

Biota of the Drinker Creek sandstone
Spirifer disjunctus
Spirifer mesastrialis
Camarotoechia aff. *C. contracta*
Camarotoechia cf. *C. horsfordi*
Dalmanella sp. cf. *D. danbyi*
Leiorhynchus sp.
Chonetes sp.
Aviculopecten sp.
Modiomorpha sp.
Leptodesma sp.
Goniophora cf. *G. chemungensis*
Loxonema? sp.
Arenicolites? sp.
Crinoid columnals
Fish plates and bones
Archeopteris?
Triturated wood

Additional collecting and laboratory preparation of the material at hand will undoubtedly augment this list considerably. Unfortunately most of the shells are not well preserved in the sandy matrix, and specific determination is usually very difficult. The fauna is essentially Wellsburgian in aspect. The general characteristics of the member are sufficiently outlined in the section, above, and in White's (1881) original description. By inference only, the beds that Willard (1936, pp. 589–591) considers the equivalent of his Luthers Mills coquinite of Bradford County, to the west of Susquehanna, may be the Drinker Creek sandstone of this report. Harding's fauna was the basis for this correlation.

The Kingsley shale, wherein *Paramphibius* occurs, is by no means "red" as the original and subsequent use of the adjective with the name would imply White (1881) brought this out in his original description of the "New Milford lower red shale." To designate it as the "Kingsley red shale member" is similarly misleading. Willard (1935, 1936), assumed this member to be of terrestrial origin. It is likely that the presence near the bottom of the member of the supposed amphibian tracks weighed heavily in drawing this conclusion. From rather careful collecting it is now possible to report that the Kingsley member in the Susquehanna area appears to carry a sparse marine fauna from top to bottom. In some layers the marine fossils are much more abundant than in others, but so is it throughout the shoreward marine magnafacies of the Chautauquan series everywhere in the embayment. Even were there zones which carried no marine fossils but were otherwise undifferentiated (Willard, 1936, pp. 588–590), it would be a grave risk to assume *per se* that they were of nonmarine origin. It is essentially true that all the marine strata of the Penn-York embayment from the Middle Devonian time on are characterized by an alternation of fossil-bearing and practically barren zones. This condition is accentuated eastward at all horizons by increasingly great nonfossiliferous zones. It is true that closer to the old shore such an alternation must be construed as an interlarding of marine and nonmarine beds. Our contention is that the site of the present Lanesboro track-bearing quarry was not that close to the ancient shore

when the Kingsley member was being deposited. The fauna so far collected from the Kingsley member is as follows:

Fauna of the Kingsley member
**Lingula* sp.
**Orbiculoidea* sp.
Spirifer disjunctus
Loxonema sp.
Goniophora sp.
Aviculopecten sp.
*Crinoid columnals (pl. 9, fig. 8)
*Nereis-like burrows
**Paramphibius didactylus*
**Corophioides* (?) n. sp.

The forms marked with an asterisk occur in direct association with the tracks of *Paramphibius*. Triturated wood occurs throughout the member in small quantity, but by no means as abundantly as in the Cascade sandstone below. I have not seen in the Kingsley any evidence of continental beds, soil horizons, or plant roots in the shale. The "Brandt" sandstone of the *Paramphibius* quarry carries a more abundant marine fauna and much more woody material than the Kingsley member.

The Starruca shale was originally differentiated by White (1881, pp. 74–75) from the overlying New Milford red shale and from the underlying "Chemung," but the draughtsman apparently (p. 77) included it by mistake with the New Milford red shale. Just where Willard would draw the boundary of his Kingsley, which is White's New Milford red under a new geographic name, is not entirely clear. However, here it is considered that the Starruca is a distinct unit, which comes at about the proper position to constitute the top of the Cayuta shale monothem. The fissile Starruca shale does not lend itself readily to fossil collecting except where locally sandy lenses have created minor scarps. However, every section of the Starruca shale in the Lanesboro area yields marine fossils. Toward the base, coquinite layers are common and readily collected in several places. The fauna that Willard lists from this member and the species in our collections all bespeak in general the Cayuta monothem. It is certain that the next unit below the Starruca, which is here correlated in general with the Owego shale to the west, carries a representative Cayuta fauna. This fauna has been given in some detail by Willard. It is likely that additional collecting will yield telling recurrent faunas such as characterize the Cayuta farther west. That the Cascade sandstone may be the equivalent of the Swartwood recurrent zone of Williams is possible from the evidence at hand. The fauna of the Cascade has been well listed by White and Willard. In places it carries prominent coquinite layers and regularly a considerable quantity of triturated wood, or even whole tree trunks, which have been carbonized. It is usually referred to as a "plant bed."

"*Facieology*."—The stratigraphic and faunal associations of the *Paramphibius* trails at Lanesboro point principally to a marine environment. On the basis of the monumental work of Barrell (1914) on the Catskill delta and more recent work by Willard (1934) on the Chemung shore line,

it has been possible to generalize (fig. 6) the hypothetical shore line at the eastern end of the Penn-York embayment during early Chemung time (solid line) and later for the Canadaway (dot-dash line) and early Conewango (dash line). The *Paramphibius* locality is indicated by a cross. The record at Lanesboro is one of migration in a shoreward (southwesterly) direction. The tracks were left on the near-shore mud flats of a bayou on the northeast side of a secondary delta, to which Willard (1934) gave the name Wyoming lobe. These paleogeographic conclusions have been reached primarily from a careful study of the direction in which the sediments grow coarser, which seems to be about the most reliable general criterion in the embayment for judging source; secondarily the general direction in which the sediments grow thicker is considered; in this latter, the direction in which the red tongues of the Catskill magnafacies (fig. 9, dotted line) grow thicker is very useful. Changes in biota are also of great importance.

It is likely that there was considerable oscillation of the strand on the shallows of the neritic zone, and an alternation of marine and brackish (or possibly even fresh water) sediments might be expected. The faunal lists have shown that red stringers overlie chiefly but also underlie the *Paramphibius* beds, and also that undeniable marine fossils occur both below and above. Plant remains occur everywhere in the Upper Devonian strata of the embayment and, in the absence of a soil zone, cannot by themselves be used to judge conditions of sedimentation. Figure 9 shows the oscillatory pattern (stippled) that everywhere in the Upper Devonian characterizes the strandline contact with the next seaward environment. Even the red beds frequently were subjected to marine reworking and now carry abundant marine faunas. In fact, the most abundant life in the embayment record frequently occurs in such red zones as Caster (1935) and Caster and Flower (1935) have discussed in some detail. The various "iron ores" of I. C. White in the Upper Devonian of Pennsylvania are usually fossil-bearing beds of the same character, as are also several of the essentially coeval coquinites mentioned by Willard. Some of the coquinites may represent death assemblages, but others, as at Lewis Run, Pa., most certainly represent a life assemblage. To assume, *prima facie*, that red beds, *per se*, connote continental environment in the Upper Devonian of the Penn-York area is highly misleading. But to carry the assumption farther and say that any beds, not red, associated with red tongues in the magnafacies zone under consideration are also, in the absence of abundant marine faunas, continental, is usually an error. It is highly probable that the whole Kingsley member in the area of Lanesboro was entirely of marine origin. To be sure these strata contain fragments of wood, but so do other beds through the whole Upper De-

vonian, even beds formed admittedly many miles from the strand as, for example, the occurrence of Dr. David White's *Protolepidodendron* and of *Callixylon* in the Rhinestreet black shale and Genundewa (Senecan are not uncommon. They occur with surprising consistency, although not exclusively, of course, in marine beds where preservation seems to have been easier than in continental environments. The Lanesboro area,

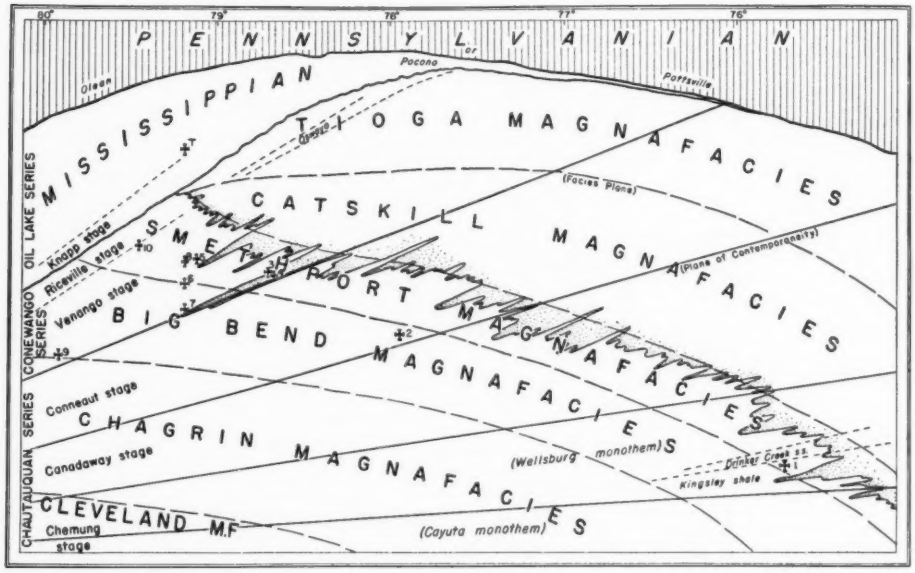

FIG. 9.—Highly generalized "facieological" diagram of the Upper Devonian strata in northern Pennsylvania, showing facies distribution of the Xiphosura and *Paramphibius*. 1. Lanesboro, Pa.: *Paramphibius;* 2. Wellsville, N. Y.: Eller's recent discovery, 1936; 3. Lewis Run, Pa.: Caster and Harris, *Protolimulus;* 4. Ridgway, Pa.: Caster, *Protolimulus;* 5. Pope Hollow, N. Y.; Caster, *Paramphibius*-like trails; 6. Warren, Pa.: Eller, "*Prestwichia*"; 7. Warren, Pa.: *Prestwichia randalli* Beecher; 8. Warren, Pa.: Tanners Hill quarry, Caster, *Protolimulus;* 9. LeBoeuf, Pa.: type *Protolimulus eriensis* (Williams); 10. Uniontown Pike, Pa.: Chestnut Ridge anticlinal inlier; Caster, *Protolimulus;* T. Warren, Pa.: *Thinopus antiquus*. (Modified from Chadwick, 1933, 1935, Caster, 1934, and Willard, 1936.)

series) limestone respectively on Canandaigua Lake, New York, or the abundance of wood in the Williams Brook limestone and Triphammer shale at Ithaca, N. Y.

From Middle Devonian time and the appearance of the first forests on earth, thin "coal seams" formed by the carbonation of lycopods, equisetales and primitive gymnosperms like almost any other Upper Devonian area between the Catskills and Lake Erie, carries much of this type of material. No seams, however small, have been observed by us in association with *Paramphibius*, nor have we observed even a carbonized trunk that might be so construed, although such a fossil might easily occur in that facies. On the other

hand, we have categorically not seen, after considerable search, any vertical plant stems, soil layers or root traces in the Kingsley shale.

The experiments with modern king crabs discussed in Part I of this paper seem to show that *Paramphibius* trails were made on moist mud. (Compare pl. 13, fig. 9, and pl. 8, fig. 7). But nowhere in the Lanesboro area have the enclosing shales shown any evidence of mud-cracking, rain drops, or other deformation usually indicative of shore conditions unless the phenomenon shown on plate 11, figure 5, is so interpreted. There is no evidence of current action or rill action, and all facts point to a very slow and very quiet accumulation of exceedingly fine grained mud and silt, possibly of lagoonal origin. A few "drag marks" such as the one shown on plate 11, figure 8, occur in the *Paramphibius* zone.

The interpretation of the *Paramphibius* environment as marine is further supported by the general correlation of the Lanesboro environment (parvafacies) with the environment of all known evidence of Limulida, either trails or remains, in the Upper Devonian of the embayment. This is shown in figure 9. That modern limuloids live in a very definite marine zone all writers on the subject seem to agree. All Devonian occurrences of Xiphosura Limulida, including *Paramphibius*, occur in one general environmental zone (the Big Bend and Smethport magnafacies) which was essentially the same one still inhabited by king crabs. The *Paramphibius* trails are unique in showing a migration out of the wholly marine life zone, shoreward into brackish water, but it is highly probable that further search of the shore zone throughout the Upper Devonian will yield many more such occurrences.

PROBLEMATICA

Abundantly associated with the trails of *Paramphibius*, but seldom in series with the tracks, are great numbers of elongate dimplings, each of which carries at the bottom an incision, which usually enters the bedding plane at less than a right angle and as low as a 45° angle. The incisions have a dumbbell-shaped surface or cross section. Several of these problematica are shown on plate 4, figure 6, and plate 11, figures 1, 2. The dimples usually occur in an alined series along their longitudinal surface axes and are connected by a cut or scoring in the strata, which seems to extend as deeply as the incisions themselves. These dumbbell-shaped incisions are most abundant in the thinly laminated sandy layers in the *Paramphibius* beds, but usually extend down into the shale below. The deepest penetration noticed was approximately half an inch. In general surficial and cross-sectional appearance, the incisions recall strongly the U-shaped worm tubes known from virtually all post-Lipalian horizons under the name of *Corophioides*. In fact, several of our specimens were referred to that genus by Dr. Othenio Abel (personal communication, March 1937). Dr. Abel has taken up the *Corophioides*

problem in some detail in his Vorzeitliche Lebensspuren (pp. 452–456), and his pronouncement naturally carries considerable weight.

These incisions seem to differ from typical *Corophioides* in several respects, the chief being the absence of a U-shaped tube and concentrically striated "Spreite." The Lanesboro markings might be compared with a *Corophioides* U without the basal arcuate part and with a smooth or vertically striated slit or split joining the parallel vertical "tubes." They seem, rather, to have been made by a sharp-bladed organ, organism or instrument, which possibly had a rounded cutting edge. Such an organ might be likened to an old-time sausage cutter with an additional beading or strengthening. This blade was apparently inserted in the bottom sediment and then withdrawn. Such a structure would account for the dumbbell-(or "Hantel") shaped cross and surface section of the incision. There is no evidence in our specimens of the arcuate base of a U-tube such as universally characterizes *Corophioides* and *Rhizocorallium*. Abel (1935) and Richter (1924) have pointed out that in both of these "genera" there is always evidence between the tubes on the same plane in which they lie, of the relict upper walls of the basal arcuate portion of the tubular U which stands more or less as a wall between the tubes as though holding them in parallel position. This structure is the "Spreite," and may be nearly as wide as the tubes themselves or a mere parting in the strata indicating the former position of the arcuate base of the ever-sinking U-tube. Such a line does connect the swollen ends of the present incisions, but on the plane no evidence of concentric striae parallel to an arcuate base of a U are to be seen. What markings are distinguishable on the "Spreite" of the present incisions seem to run vertically as though made during insertion and withdrawal of a blade. Furthermore, there seems to be good evidence not of the slow abrading action of a marine worm in a U-shaped burrow but of the forceful insertion of a blade with concomitant deformation of the penetrated strata. The surface is always depressed in a dimple and the underside of the beds are downwardly deformed as shown by the figures. Moreover, there is almost invariably a slight amount of "normal faulting" associated with each incision, which is very similar to the "faulting" that occurs when a putty knife or razor blade is forced into soft putty or modeling clay and withdrawn under very slight horizontal pressure. The side pressed against tends to adhere to the blade and to be elevated slightly above the other side of the incision when the blade is withdrawn. Compare the figures on the plates of this paper with those of Abel in Vorzeitliche Lebensspuren (figs. 378–381, pp. 453–455), and the differences between our incisions and those of the European *Corophioides* become rather clear. See also fig. 1, *k* and *kk* of this paper.

From the possibly deceptive appearance of an organism or organ having moved over the surface and

intermittently punched holes in the mud, and from the association solely with *Paramphibius*, the entirely speculative and tentative suggestion is offered that these incisions may have been made by a female opercular plate used as an ovipositor after the manner that has been suggested (Kingsley, 1892, p. 36) for *Limulus polyphemus*. If this is the explanation, then *Paramphibius* must have had an opercular plate of much the general shape recorded for *Protolimulus* from the Devonian, as has been brought out above. (Compare pl. 8, fig. 6, with pl. 12, fig. 7.) The oviducts were quite likely more laterally located on the operculum of early Xiphosura than on the recent forms, if ontogenetic evidence in this matter has any bearing. Sheaths of oviducts so located may have made tubelike punctures on either side of the opercular plate incision during the process of oviposition. Against this theory as also against the *Corophioides* interpretation, is the presence of a "Spreite"-like cut, shown on plate 11, figure 3, which joins the incisions from dimple to dimple in longitudinal series. Such a continuing line, if of primary origin, suggests more the work of a clam that moved along in a half submerged manner and occasionally dug in more deeply, the while exserting a pair of siphons. No clams are known, however, from the *Paramphibius* beds, and similar incisions are not yet known in America dissociated from *Paramphibius*. Certainly our incisions have little in common, beyond superficial dumbbell cross section, with the Upper Devonian *Corophioides*, which Hecker (1930) describes from the Wolchow River district of Russia.

SUMMARY

The conclusions reached in this paper are: 1. *Paramphibius* trails were made by an ancestral king crab (Limulida) having the general anatomical organization of modern *Limulus*, and very similar organization to the representatives of the Limulida in the Upper Devonian. 2. The trails of *Paramphibius* are strikingly similar to those made by modern *Limulus*, the most significant feature of which is a heteropod condition resulting from the use of three or four pairs of simple chelate feet and one pair of pushers in ordinary walking. 3. The trails associated with Paleozoic limuloids are very similar to those of *Paramphibius*. 4. In view of the fact that modern king crabs walk extensively only during the limited mating season in the spring, and that *Paramphibius* tracks occur in an environment closely similar to a modern shore of the type sought out by the mating limuli, the conclusion is reached that the reason for the Lanesboro tracks lies in the age-old mating urge. 5. *Paramphibius* lived in precisely the same facies-band (magnafacies) or "fossil environment" as all known Upper Devonian Limulida of the Penn-York embayment. 6. This environment was marine, and essentially like that still occupied by Xiphosura Limulida. 7. Systematically, *Paramphibius* had best be considered (especially in view of the inappropriateness of the name)

as an ichnological form-genus. 8. It is probably only a more complete trail of the same type that is imperfectly known by the imprints in the Upper Devonian that are associated with fossil Limulida, such as *Merostomichnites*. 9. *Paramphibius* seems to be generically distinct from *Merostomichnites*, s.s. 10. Apparently the type trails of *Paramphibius* were all made by different-sized individuals of the same species of Limulida, and therefore only one species of trail (*Paramphibius didactylus* Willard) in the type occurrence should be recognized. 11. The maker of *Paramphibius* trails, when found, will probably be closely related to, if not identical with, *Protolimulus* (and/or forms in the Upper Devonian assigned to *Paleolimulus*). 12. Finally, the reinterpretation of *Paramphibius* leaves the North American Devonian without any evidence of the Amphibia.

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The trails were first interpreted as limuloid by Prof. E. L. Petry and Miss Ruth Petry who in 1935 was a student in historical geology. Their continued interest in the problem is appreciated. Through the courtesy of Mr. L. C. Boochever, of the Department of Publicity at Cornell University, considerable interest in the problem was aroused and much valuable field assistance obtained.

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The material on which this study is based is deposited in the Museum of Paleontology, at the University of Cincinnati. A duplicate collection is on deposit at the Paleontological Research Institution, Ithaca, N. Y., and another collection was presented to Cornell University in 1935.

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OPHIURANS FROM THE UPPER SENONIAN OF SOUTH LIMBURG, HOLLAND

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ABSTRACT

Twenty-five kinds of detached ophiuran plates are grouped into four new species representing four genera, of which two, *Platyarthra* and *Dolicharthra* are new.

Early in the fall of 1935 the author received a large quantity of fossil ophiuran material from Dr. J. H. Bonnema, of Gröningen, Holland, which he had collected from beds of Senonian age in South Limburg. This paper deals with the description and identification of the disarticulated plates of the four species included in the material. The types are deposited at the Johns Hopkins University.

The author wishes to express his deepest thanks to Dr. Bonnema for permission to study this material and for the assistance he has rendered in the preparation of this paper. Thanks are also due to Dr. Th. Mortensen for the specimens of recent ophiurans that were used in connection with this study. To the Geological Society of America the author is indebted for a Penrose Grant, which was used to complete the illustrations.

Beds of Upper and Lower Senonian (Cretaceous) age crop out in the southernmost part of South Limburg, Holland. There appears to be some dispute as to the exact placement of certain members of the Upper Senonian. The one presented here is taken in part from the work of Van Veen (1) and from information received from Doctor Bonnema.

Upper Senonian
- Maastrichter Tuffkreide
  - first bryozoan layer
  - second bryozoan layer
  - third bryozoan layer of Staring
  - third bryozoan layer of Ubaght
- Gulpenes chalk

The Maastrichter Tuffkreide consists of various beds of chalk containing scattered chert nodules. In the upper part of this formation are four different bryozoan layers, distinguishable by their fossils. Staring and Ubaght disagree as to the exact age and placement of the third bryozoan layer. In this paper the third layer of Ubaght is designated the fourth.

The lowest bed, composed predominantly of coprolites, is about 2 inches thick. The next 65 feet is very loose chalk with definite thin beds of flintstones running through it. Above this is 32 feet of loose chalk containing irregularly scattered flintstones and two definite bryozoan layers, one very near the bottom of the bed and the other near the center. Overlying this is 65 feet of the same loose

chalk barren of any flintstone. This bed contains two bryozoan layers, one near the base and the other near the top. The average thickness of each bryozoan layer is about 18 inches.

The minute calcareous plates of ophiurans were found in the bryozoan layers at several places. The first bryozoan layer yielded plates at three localities in and around the town of Bemelen, near Maastricht. Collections from the second and third layers were made in a quarry in the valley of the Jeker River. Collections from the fourth layer came from a quarry at Valkenburg and also from two quarries near the town of Kunrade. Most of the plates show the true reticulate structure of ophiuran plates, but those from Bemelen have a vitreous appearance and do not show their structure. They appear to have been subjected to secondary replacement. Whether the original plates were dissolved out and calcite redeposited in the cavities or whether the minute openings in the original plates were filled with calcite is uncertain. The latter is more probable, for the matrix of these plates is not favorable for preservation of the minute details, which remain on the vitreous plates as well as on the spongy ones. Similar replacement is shown in the ostracods (2).

With the ophiurans are numerous other microfossils, some though not all of which are recognizable. The most numerous by far are joints from the arms of crinoids, like those in the comatulid group. The order Phanerozonia of the asteroids is represented by various large arm plates. A great many spines, ambulacral plates, and brace plates representing several species of echinoids are present, as well as young echinoids 1 to 2 mm. in diameter. Van Veen reports that these deposits are full of ostracods, but the present author did not observe any in the material at his disposal. The material includes minute fish teeth and a great quantity of coprolites, both the usual capsule-shaped fish type and another type totally different and of unknown origin.

Comparison of the plates from different localities reveals that all those from one of the three collections from the first bryozoan layer and all from one of the three collections from the fourth layer are proportionately larger than those from other places. This fact appears to indicate that living conditions were more favorable at those two places than elsewhere. None of the large plates were selected for illustration because they would appear out of proportion to the associated plates of the same species.

In order to ascertain how many species are represented by the detached plates, the plates were first sorted into groups of similar kinds—vertebral ossicles, dorsal arm plates, etc.; then each group was separated into separate varieties—25 in all out of 24,657 plates. Each kind is designated by a different letter in the accompanying table and in the systematic descriptions. Examination of the table shows that there are four kinds of vertebral ossicles, four kinds

of ventral arm plates, four kinds of lateral arm plates, and four kinds of radial shields. It may therefore be assumed that at least four species are represented in the material examined.

It likewise seems evident that the quantity of each kind preserved would normally be proportional to the abundance of the species it represents. However, the accidental local accumulation of detached parts may result in an abnormal quantity of certain plates. This seems to have been the case at the places where collections were made from bryozoan layer 4.

Application of the statistical method to the vertebral ossicles and arm plates enumerated in the table results as follows:

	Bryozoan layer			
	1	2	3	4
Vertebral ossicles	B	B	B	B
Dorsal arm plates	F	F	F	E
Ventral arm plates	I	H	H	I
Lateral arm plates	L	L	L	L

Distribution of ophiuran plates

Bryozoan layer		1	2	3	4	Total
Vertebral ossicle	A	34	43	6	3	86
	B	1,580	334	281	926	3,121
	C	5	6	71	44	126
	D	4	4	—	—	8
Dorsal arm plate	E	143	9	9	2,292	2,453
	F	319	144	33	5	501
	G	1	—	—	—	1
Ventral arm plate	H	102	200	52	257	611
	I	134	44	11	339	528
	J	—	—	—	3	3
	K	—	13	—	—	13
Lateral arm plate	L	1,309	1,473	410	12,156	15,348
	M	200	—	44	580	824
	N	108	86	10	4	208
	O	—	3	3	123	129
Comb plate	P	52	10	7	324	393
Radial shield	Q	1	—	—	4	5
	R	1	1	9	191	202
	S	1	—	—	—	1
	T	1	—	—	2	3
Disk plate	U	1	—	—	73	74
Oral shield	V	—	—	—	2	2
	W	2	1	—	—	3
Jaw	X	—	—	—	4	4
Genital plate	Y	—	—	—	10	10
Total		3,998	2,371	946	17,342	24,657

This indicates that the parts normally most abundant are B, F, H, and L, which presumably belong to the same species (*Ophiura kunradeca*), and that bryozoan layer 4 contains an abnormally large proportion of plates E, I, and L, and a scarcity of F.

The second grouping in order of abundance is as follows:

	Bryozoan layer			
	1	2	3	4
Vertebral ossicles	A	A	C	C
Dorsal arm plates	E	E	E	F
Ventral arm plates	H	I	I	H
Lateral arm plates	M	N	M	M

This shows a normal association of plates E, I, and M with either A or C; but C is eliminated because the dorsal arm plates are very rudimentary or wanting in living species having vertebral ossicles like C. The second species (*Platyarthra jekerica*) therefore presumably includes plates A, E, I, and M. There is an abnormal abundance of C in layers 3 and 4, and of N in layer 2.

Similarly, the third grouping is as follows:

	Bryozoan layer			
	1	2	3	4
Vertebral ossicles	C	C	C	C
Dorsal arm plates	G	—	—	—
Ventral arm plates	—	K	—	J
Lateral arm plates	N	O	N	O

This indicates that C and N belong to a third species (*Asteronyx valkenburgensis*), which may include also G and either J or K. But as no living forms with vertebral ossicles like C have ventral arm plates like J or K, the former being merely an adoral modification of I, and therefore referred to the second species, J and K are eliminated.

Plates belonging to the disk are rare in all the layers except 4. Application of the statistical method to them indicates that comb plate P, radial shield R, oral shield V, jaw X, genital plate Y, and probably disk plate U should be grouped together, and presumably belong to species 1, whose living relatives have comb plates, radial shields, and genital plates. Of the remaining plates, Q and W probably belong together and may represent species 2. Plate S presumably belongs to species 4 because it is unlike the radial shield plates of living relatives of species 3. This leaves plate T for species 3.

During the Mesozoic era the Ophiuroidea were more numerous than at any other time in their geological history. Their zenith was apparently reached in the Jurassic period; they declined in the Cretaceous; and the Tertiary opened with very few representatives. This at least is the record as shown by their fossil remains —a record that is probably erroneous, because conditions for preservation of their delicate plates may have been ideal only in Jurassic time and because these organisms have been neglected by paleontologists in recent years. Only about fifteen species of ophiurans have been reported from the Cretaceous deposits of the world. Of this number only four were collected in the United States, the remainder coming from European beds. The Cretaceous ophiurans of the United States fall into the genera *Amphiura* and *Ophioglypha*, the latter embracing three species. In the current classification of recent ophiurans the genus *Ophioglypha* is not recognized, having been replaced by the genus *Ophiura* and other allied genera. The nomenclature of the Cretaceous genera is likewise in need of revision.

The Cretaceous ophiurans of Europe are grouped under the genera *Amphiura*, *Ophiura*, *Geocona* and

Ophiotitanos, the last two genera being represented by fossil forms only. Four of the European species have been reported from the Cretaceous of England, the remainder come from various localities on the Continent. As none of the individual plates of these Cretaceous ophiurans have been described separately, only fragmentary parts of the arms or disk, the previous work is of very little assistance in the study of the detached plates.

Representatives of the order Euryalae, with their hourglass-shaped articulating vertebral ossicles, living in the northeast Atlantic waters are restricted to the three families Asteronychidae, Goryonocephalidae and Asteroschematidae. The Goryonocephalidae have branching arms; vertebral ossicles of those segments where bifurcation takes place have double articulating surfaces. None of this type of ossicle was found among the 126 having hourglass-shaped articulating-surfaced ossicles from the four bryozoan layers, nor were there found fossil any of the minute hooks that are common on the arms of this family.

The Asteroschematidae are represented by two species (3) in the European region, *Asteroschema inornatum* and *Ophiocreas oedipus*, both living in water deeper than 1,000 meters off Madeira. *A. inornatum* is also found at about the same depth in the Bay of Biscay. Because of their present distribution and their deep-water habitat it seems highly improbable that the fossil species are related to the representatives of this family living in European waters today.

Two species of the Asteronychidae, *Astrodia tenuispina* and *Asteronyx loveni* live today in European waters. The former is restricted to southern European waters, whereas the latter has practically a world-wide distribution. The vertebral ossicles of *Asteronyx loveni* show a very close similarity to the fossil vertebral ossicles of the C type, which have been shown to be associated with the N type of lateral arm plates. No such lateral arm plates were found in the living species *A. loveni*. The supposed association of the C and N plates may be incorrect, or the Cretaceous progenitor of this species may have had lateral arm plates, which its descendants lost in adapting themselves to curling up their arms.

Klinghardt (4) has described a fossil ophiuran from the Lower Senonian to which he has given the name *Ophiura furstenbergii*. This fossil is coiled like the living species of the order Euryalae, which would lead one to believe that it probably has hourglass-shaped articulating surfaces and should not have been placed under the genus *Ophiura*. It is probably congeneric with the species herein described as *Asteronyx valkenburgensis*.

SYSTEMATIC DESCRIPTIONS

ASTERONYX VALKENBURGENSIS C. Berry, n. sp.

Plate 16, figures 13–16, 19, 22–25

This species is composed of plates C, N, and T. It has been placed in the genus *Asteronyx* because of the articulating surfaces of its vertebral ossicles. The spe-

cific name is taken from the town of Valkenburg, South Limburg, Holland, near which most of the plates belonging to this species were found.

Radial shield T.—(Pl. 16, figs. 22, 25.) Outline oval; outer surface swollen, arched transverse to long axis of plate; inner surface cumulating into a ridge, which crosses the center of the plate parallel to long axis. Length, 1.76 mm.; width, 1.12 mm.; thickness, 0.48 mm.

Lateral arm plate N.—(Pl. 16, figs. 23, 24.) Outline modified crescent with offset on ventral part of aboral margin; outer surface smooth, convex, transverse to short axis of plate; aboral margin slightly rough. Inner surface concave, paralleling curvature of plate; aboral edge thick, thinning towards dorsal and ventral margins, adoral edge thin. Height, 1.20 mm.; width in middle, 0.64 mm.

Vertebral ossicle C.—(Pl. 16, figs. 13–16, 19.) Adoral view: Outline circular, indented on both dorsal and ventral sides by canal furrows. Surface sloping toward margins. Dorsal center of adoral face having a vertically raised hourglass-shaped articulating surface. whose dorsal and ventral ends are rounded. A fine groove runs vertically across this surface.

Aboral view: Outline circular; surface sloping toward margins; dorsal center of aboral face having a transversely raised hourglass-shaped articulating surface whose lateral ends and edges are rounded.

Lateral view: Outline irregular, dorsal part of aboral side occupied by hourglass-shaped articulating surface; adoral side occupied by entire hourglass-shaped articulating surface; surface of plate rounding down to margins; plate thicker near dorsal edge than ventral edge.

Dorsal view: Outline irregular, top of hourglass-shaped articulating surface seen on adoral side; aboral side occupied by entire hourglass-shaped articulating surface; surface rounded, very irregular. Across center on dorsal part of plate is shallow upper canal furrow parallel to axis of plate.

Ventral view: Outline same as in dorsal view. Surface more acute; deep lower canal furrow crosses center of ventral portion of plate parallel to axis of plate.

Length, 1.12 mm.; width, 1.2 mm.; height, 0.8 mm.

Ophiura kunradeca C. Berry, n. sp.
Plate 14, figures 1–10, 13–25

This species is composed of plates B, F, H, L, P, R, U, V, Y, and X. It has been placed in the genus *Ophiura* because of its peculiar vertebral ossicle. The specific name is taken from the town of Kunrade, South Limburg, Holland, near which most of the plates belonging to this species were found. *O. kunradeca* is the most abundant species in the collection.

Disk plate U.—(Pl. 14, figs. 8, 9.) Outline modified cardioid. Dorsal surface arched, ventral surface flat. Thicker in center, thin at edges.

The collections contain many disk plates with the same general shape but not exactly alike.

Radial shield R.—(Pl. 14, figs. 18, 21.) Outline modified rectangular, corners rounded. Dorsal surface smooth, slightly arched transverse to short axis, edges rounded. Aboral two-thirds of inside lateral margin has a deep groove that gives

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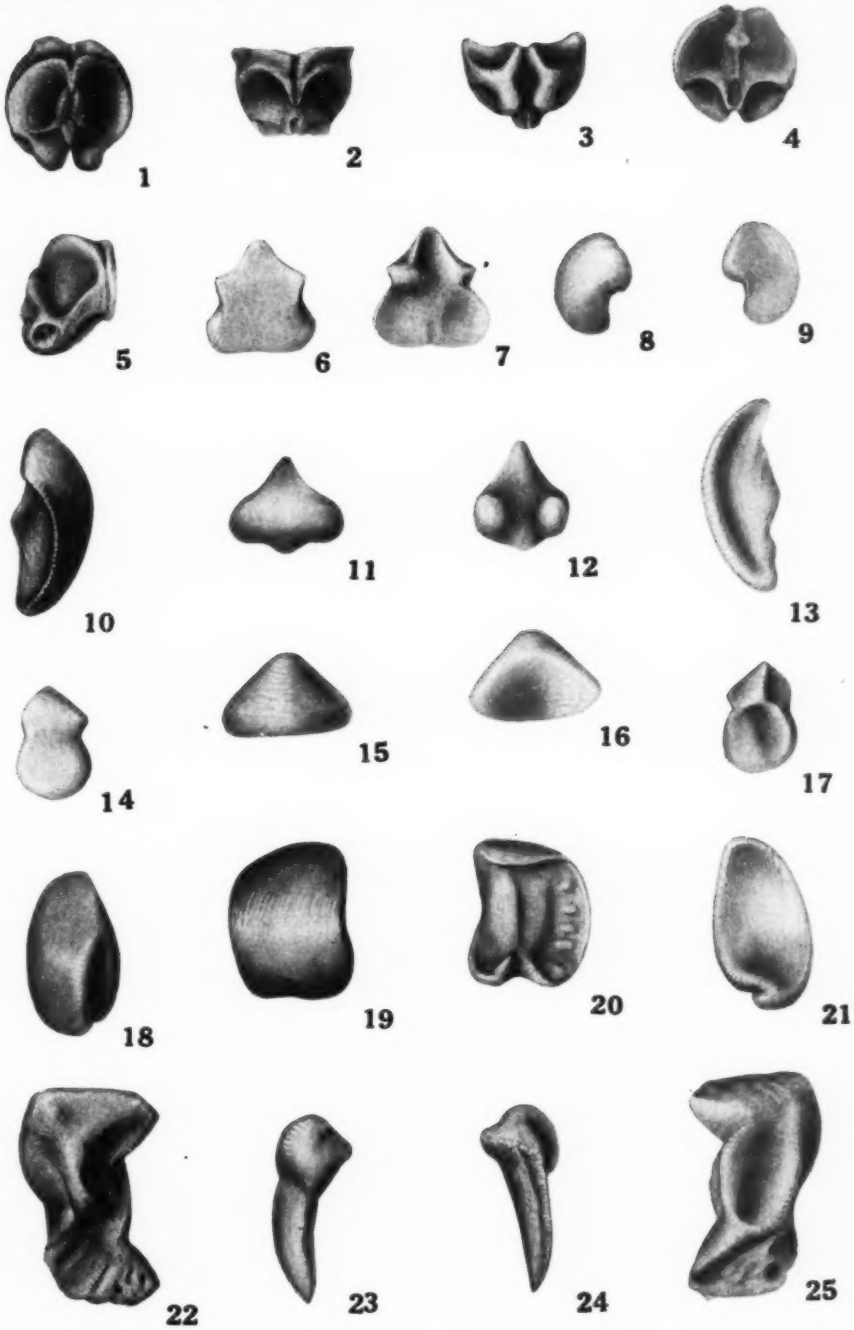
Explanation of Plate 14

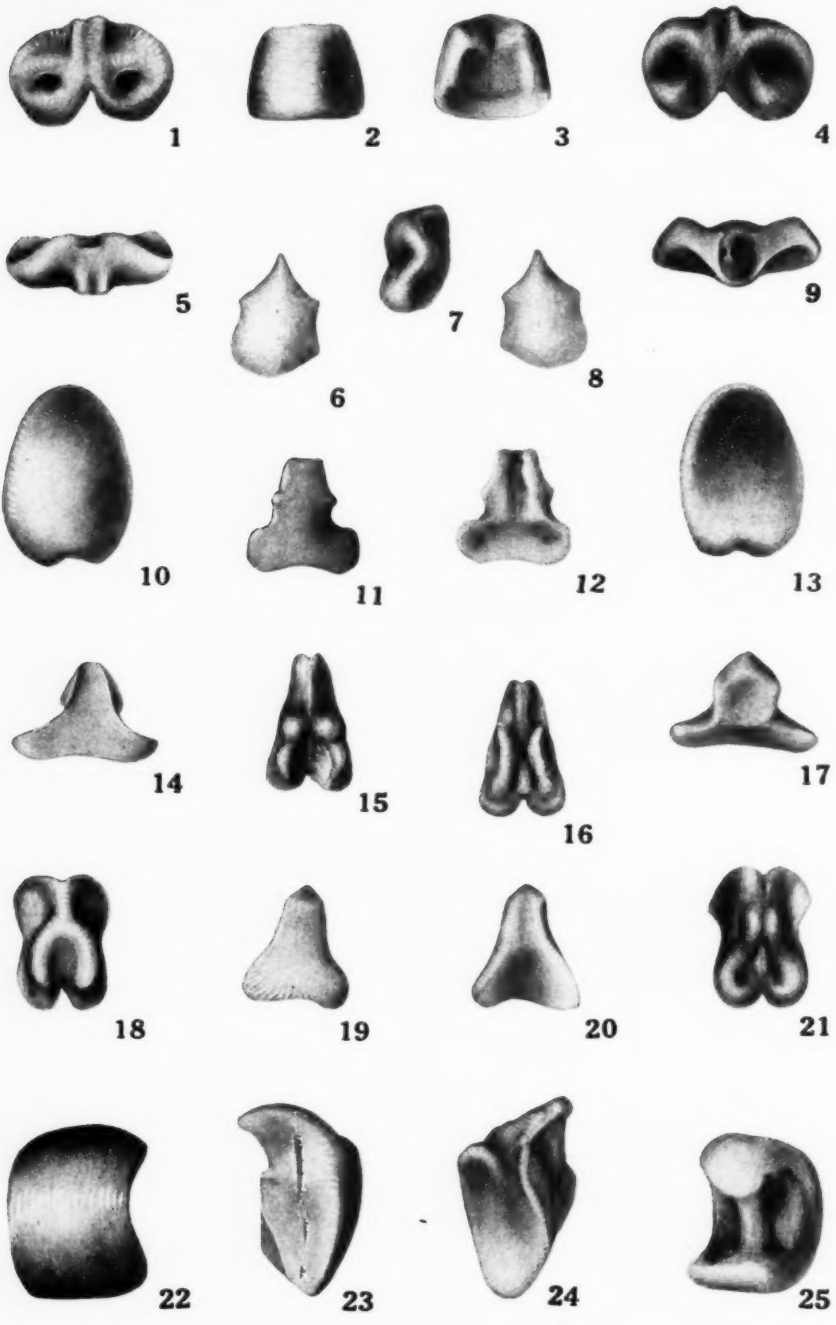
Figs. *1–10, 13–25—Ophiura kunradeca* C. Berry, n. sp. *1–5*, Aboral, dorsal, ventral, adoral, and lateral views of vertebral ossicle B. *6, 7*, Ventral and dorsal views of ventral arm plate H. *8, 9*, Dorsal and ventral views of disk plate U. *10, 13*, Views of comb plate P. *14, 17*, Ventral and dorsal views of oral shield V. *15, 16*, Dorsal and ventral views of dorsal arm plate F. *18, 21*, Dorsal and ventral views of radial shield R. *19, 20*, Outside and inside views of lateral arm plate L. *22, 25*, Outside and inside views of jaw X. *23, 24*, Dorsal and ventral views of genital plate Y.

11, 12—Genus and species undetermined. Views of different arm plates.

All figures approximately ×14.



C. Berry, Senonian Ophiurans



C. Berry, Senonian Ophiurans

adoral-lateral corner an offset angle. Area outside of groove probably covered by abutting plate. Ventral surface concave to conform with external surface. Raised area near aboral-inside lateral corner. This raised area acts as condyle for articulation of plate. Plate much thinner along outside lateral margin than inside lateral margin. Length, 1.52 mm.; width, 0.88 mm.; thickness, 0.4 mm.

Comb plate P.—(Pl. 14, figs. 10, 13.) The exact orientation of this plate is uncertain. Outline modified crescent. High crescent-shaped ridge paralleling right margin, crossing plate; surface sloping evenly towards right margin from ridge, left lateral surface concave, forming deep depression; right lateral surface flat; slight raised ridge along curved side. Length, 1.84 mm.; width, 0.72 mm.

Dorsal arm plate F.—(Pl. 14, figs. 15, 16.) Outline modified triangle with rounded corners, lateral margins converge into adoral apex; aboral margin convex; lateral margins thicker than aboral margin; dorsal surface swollen, rounding down to straight lateral sides; ventral surface concave. Length, 0.88 mm.

Oral shield V.—(Pl. 14, figs. 14, 17.) Outline irregular, adoral end pointed, aboral end rounded, slight depression about half way down lateral sides; ventral surface smooth; dorsal surface irregular, having a ridge in the adoral one-third, from which surface slopes toward adoral-lateral margins. Area of rest of plate flat, at a slightly lower level than ridge. Length, 1.04 mm.; width, 0.72 mm.

Ventral arm plate H.—(Pl. 14, figs. 6, 7.) Outline modified triangle; aboral margin curved; lateral margins deeply bisunate, meeting in acute flat point at adoral end. Ventral surface slightly swollen, rounding towards dorsal side on lateral margins; adoral apex very thin, and appearing as if covered by preceding plate; dorsal surface irregular, having a broad shallow groove running from adoral apex towards aboral margin; aboral half of plate sloping to thin aboral margin; adoral half of lateral sides rounding down towards ventral side of plate. Length, 0.96 mm.; width, 1.04 mm.

Lateral arm plate L.—(Pl. 14, figs. 19, 20.) Outline modified rectangular, aboral-dorsal corner rounded, aboral margin convex, adoral concave, ventral and dorsal straight; outer surface smooth, arched transverse to axis of arm; outer surface sloping down to adoral and aboral margin from diagonal ridge across plate near adoral margin; indented a short distance from aboral margin by four flattish oval areas of different sizes, largest one near ventral margin. In recent forms they are used as areas of articulation with the plate that they overlap. Deep semicircular pit a little aboral of center on ventral margin. Ventral margin sharp ridge; flattish. Height, 1.52 mm.; width in center of plate, 1.20 mm.

Jaw (right jaw) X.—(Pl. 14, figs. 22, 25.) Outline semirectangular; adoral margin straight; aboral margin rounding into ventral margin, which has centrally located shallow sinus; dorsal margin bisunate, making acute angle with adoral and aboral margin; outer surface irregular, having a central short steep-sided

EXPLANATION OF PLATE 15

FIGS. *1–14, 17, 22, 25—Platyarthra jekerica* C. Berry, n. gen. and n. sp. *1, 4, 5, 7, 9*, Aboral, adoral, dorsal, lateral and ventral views of vertebral ossicle A. *2, 3*, Dorsal and ventral views of dorsal arm plate E. *6, 8*, Dorsal and ventral views of oral shield W. *10, 13*, Dorsal and ventral views of radial shield Q. *11, 12*, Outside and inside views of ventral arm plate I. *14, 17*, Outside and inside views of ventral arm plate J. *22, 25*, Outside and inside views of lateral arm plate M.

15, 16, 18–21, 23, 24—Genus and species undetermined. *15, 16*, Two views of same vertebral ossicle. *18, 21*, Two views of the same vertebral ossicle. *19, 20*, Outside and inside views of the arm plate. *23, 24*, Outside and inside views of the same plate.

All figures approximately ×14.

ridge from which surface slopes steeply on dorsal, ventral, and aboral sides. Aboral end of ridge slightly swollen. Shallow groove at aboral end of ridge curving adorally toward the dorsal side and cutting margin in deep U-shaped groove (for circumoesophageal nerve-ring) about one third distance from adoral end. Aboral part of outer surface covered by dorsal-aborally directed grooves and ridges, which form articulating surface with other part of jaw. Ventral of these is broad shallow similarly directed groove terminating near aboral end of central ridge. Inner surface more regular, center portion occupied by depressed area, deeper near aboral end. Aboral third sloping diagonally towards outside and articulating with the first vertebral ossicle. Surface of plate in general arched along long axis of plate. Margins rounded. Length, 2 mm.; height, 1.12 mm.; thickness, 0.64 mm.

Genital plate Y.—(Pl. 14, figs. 23, 24.) Outline stylate with sharp adoral end; aboral end swollen by articulating process; ventral surface uneven, with groove running down side; ventral side of groove high; narrow ridge crossing the entire length of the plate; dorsal surface sloping down from central ridge to lateral edges. Surface of aboral swollen process uneven but with no definite configuration. Length, 1.76 mm.; width at aboral end, 0.72 mm.

Vertebral ossicle B.—(Pl. 14, figs. 1–5.) Adoral view: Outline circular, ventral side indented by deep U-shaped lower canal furrow; surface of ala concave with central area of articulation; adoral side of posterior hypapophyses occupying depression in lateral-ventral corners; articulating surface consisting of small obcordate central condyle, ventral of which is deep narrow steep-sided depression or socket, flanking which on lateral sides are two raised toothlike areas.

Aboral view: Outline same as in reverse view. Surface uneven, center occupied by highly raised articulating area consisting of centrally located zygosphene flanked dorsally by two zygocondyles; zygosphene and zygocondyles about same size, twice as long as wide; lower canal furrow indents ventral margin as deep U-shaped groove; upper canal furrow is shallow V-shaped groove; anterior hypapophyses flanking lower canal furrow. Parapophyses concave, sloping toward lateral margin of plate; upper alar ridge exposed above dorsal edge of parapophyses.

Lateral view: Outline irregular; dorsal margin straight, forming angle of about 90° with adoral margin; adoral margin straight, lower half curving down and forming ventral margin; aboral margin interrupted by zygosphene and dorsally located zygocondyles. None of the articulating processes on the adoral side are visible in this view. Most of surface is occupied by concave parapophysis.

Dorsal view: Outline modified equilateral triangle whose base is adoral; adoral margin has centrally located shallow sinus; lateral margin convex; aboral margin irregular owing to rounded anterior hypapophyses forming lateral corners; zygosphene centrally located. Surface uneven; dorsal edge of parapophysis and upper alar ridge enclosing slightly depressed area; concave parapophysis forming part of aboral part of dorsal surface.

Ventral view: Outline same as in reverse view. Surface very uneven, with centrally located steep-sided, deep U-shaped lower canal furrow occupying aboral part of plate. Posterior hypapophysis dividing the lateral section into two parts. Anterior hypapophysis present at aboral corner. Zygosphene in center of aboral side. Length, 0.96 mm.; width, 1.12 mm.; height, 0.88 mm.

Genus PLATYARTHRA C. Berry, n. gen.

Genotype *Platyarthra jekerica* C. Berry

PLATYARTHRA JEKERICA C. Berry, n. sp.

Plate 15, figures 1–14, 17, 22, 25

This species is composed of plates A, E, I, M, J, Q, and W. The generic name *Platyarthra*, meaning broad joint,

has been chosen because of the vertebral ossicle A. The specific name was taken from the Jeker River of South Limburg, Holland, in whose valley most of the plates of this species were collected.

Radial shield Q.—(Pl. 15, figs. 10, 13.) Outline oval, aboral margin cut by a shallow median sinus. Outer (dorsal) surface swollen; lateral and adoral edges beveled, showing evidence of overlapping of abutting plates. Inner (ventral) surface slightly concave, with raised area of articulation near aboral margin; aboral margin steeply beveled. Length, 1.6 mm.; width, 1.20 mm.

Dorsal arm plate E.—(Pl. 15, figs. 2, 3.) Outline a modified truncated triangle with rounded corners; adoral margin shorter than aboral; plate strongly arched transverse to long axis. Adhering to surface of central part of plate is foreign matter, which gives the illusion of two grooves crossing the plate, the right one appearing deeper, owing to shadows on the plate. Inner surface conforming with curvature of external surface; sloping to thin aboral margin. Lateral margins thick, giving evidence of straight line of contact with lateral arm plates; adoral margin thin. Length along center line, 0.96 mm.; width across adoral end, 0.80 mm.; thickness adorally, 0.40 mm.

Oral shield W.—(Pl. 15, figs. 6, 8.) Outline irregular; aboral margin irregularly convex; adoral apex acute; lateral margin straight except in adoral-lateral region, where it is concave. Outer (ventral) surface slightly swollen. Apex asymmetrical in position. Inner (dorsal) surface strongly swollen; highest point in center, where it is slightly flattened as if for attachment for muscle. Width, 0.80 mm.; length from adoral apex to aboral margin, 1.04 mm.

This plate is regarded as an oral shield because it apparently overlapped neighboring plates and because of its region for muscular attachment.

Ventral arm plate I.—(Pl. 15, figs. 11, 12.) Outline modified triangle with very broad aboral base, having shallow sinus in center and rounded lateral corners. Adoral margin straight; about one-third as wide as aboral; lateral sides of plate bisinuate, adoral one shallow, aboral one deep, with rounded margins. Outer surface smooth, with slightly rounded margins; inner surface uneven, aboral third slanting to thin aboral margin; broadly centrally grooved on adoral two-thirds. Lateral sides of plate steep. Width, 1.12 mm.; length, 1.08 mm.

Plate I differs markedly from other lateral arm plates described.

Ventral arm plate J.—(Pl. 15, figs. 14, 17.) Outline modified equilateral triangle with concave sides and rounded corners. Base or aboral margin shallow, sinuate centrally, margin curving around to form lateral corners. Lateral sides strongly concave; flanged near rounded adoral apex. Outer (ventral) surface flat and smooth; inner surface very uneven; steeply beveled along aboral margin; slightly concave adorally with sides sloping diagonally toward adoral lateral part of margin. Surface of lateral margin concave, sloping adorally. Plate much thicker in center than along the margins. Width, 1.36 mm.; length, 0.88 mm.

Plate J is probably either the first or second ventral arm plate, a modification of plate I.

Lateral arm plate M.—(Pl. 15, figs. 22, 25.) Outline modified rectangle; aboral margin convex, adoral margin concave; dorsal and ventral margins straight. Outer surface smooth, arched transverse to axis of arm; inner surface in general concave; flattened along both the dorsal and ventral margins. Sides of the ventral flat area parallel; ventral side of the dorsal flat area has near its adoral end a very large lobe from which a low rounded ridge extends diagonally across to the aboral ventral corner of the plate. From this ridge the sides slope toward the adoral and aboral margins of the plate, adoral slope being a little steeper than the aboral. Height, 1.68 mm.; width, 1.12 mm.

This type of lateral arm plate might be just a variety of the L type, but there appears to be no gradation from one type to the other in the approximately 16,172 lateral arm plates examined.

Vertebral ossicle A.—(Pl. 15, figs. 1, 4, 5, 7, 9.) Adoral view: Outline modified rectangle, corners rounded, ventral side indented by deep V-shaped lower canal furrow. Surface uneven; a broad shallow depression in middle of dorsal margin decreasing in depth toward center of plate, where it disappears; large oval depression in central part of right and left halves; smoothly rounded raised area ventral to each of these hollows. These depressions and raised areas coincide with those on the next ossicle.

Aboral view: Outline same as in reverse view. Surface uneven, with a medial broad area with parallel sides running from the dorsal margin of plate to lower canal furrow, where it divides, forming lateral margin of canal furrow, decreasing in height until it disappears at ventral margin. A shallow groove running down the middle of this ridge appears to be the line of contact of the right and left halves of the plate, but none of the fossils collected have been broken along this line. The surface of a horizontal raised area crossing the plate dorsal of this ridge slopes gently adorally, but the ventral side is steeper.

Lateral view: Outline rectangle; surface uneven; right and left halves appear as sigmoid in shape in this view, with nearly parallel sides.

Dorsal view: Outline rectangle, adoral side long; surface uneven, adoral side vertical with rounded raised area forming corners of rectangle. Aboral side sloping up adorally except in center, where there is a flat raised ridge. The actual curvature of the dorsal surface can be discerned.

Ventral view: Outline same as in reverse view. Surface broken in center by deep, broad V-shaped lower canal furrow. On flank of each side of this canal furrow can be seen the minute foramen for the canal for the podia. Ventral part very thin near the lateral margins of the plate, becoming thicker toward the center.

Length, 0.64 mm.; width, 1.64 mm.; height, 0.64 mm.

Genus DOLICHARTHRA C. Berry, n. gen.

Genotype: *Dolicharthra bemelenica* C. Berry

DOLICHARTHRA BEMELENICA C. Berry, n. sp.

Plate 16, figures 1–12

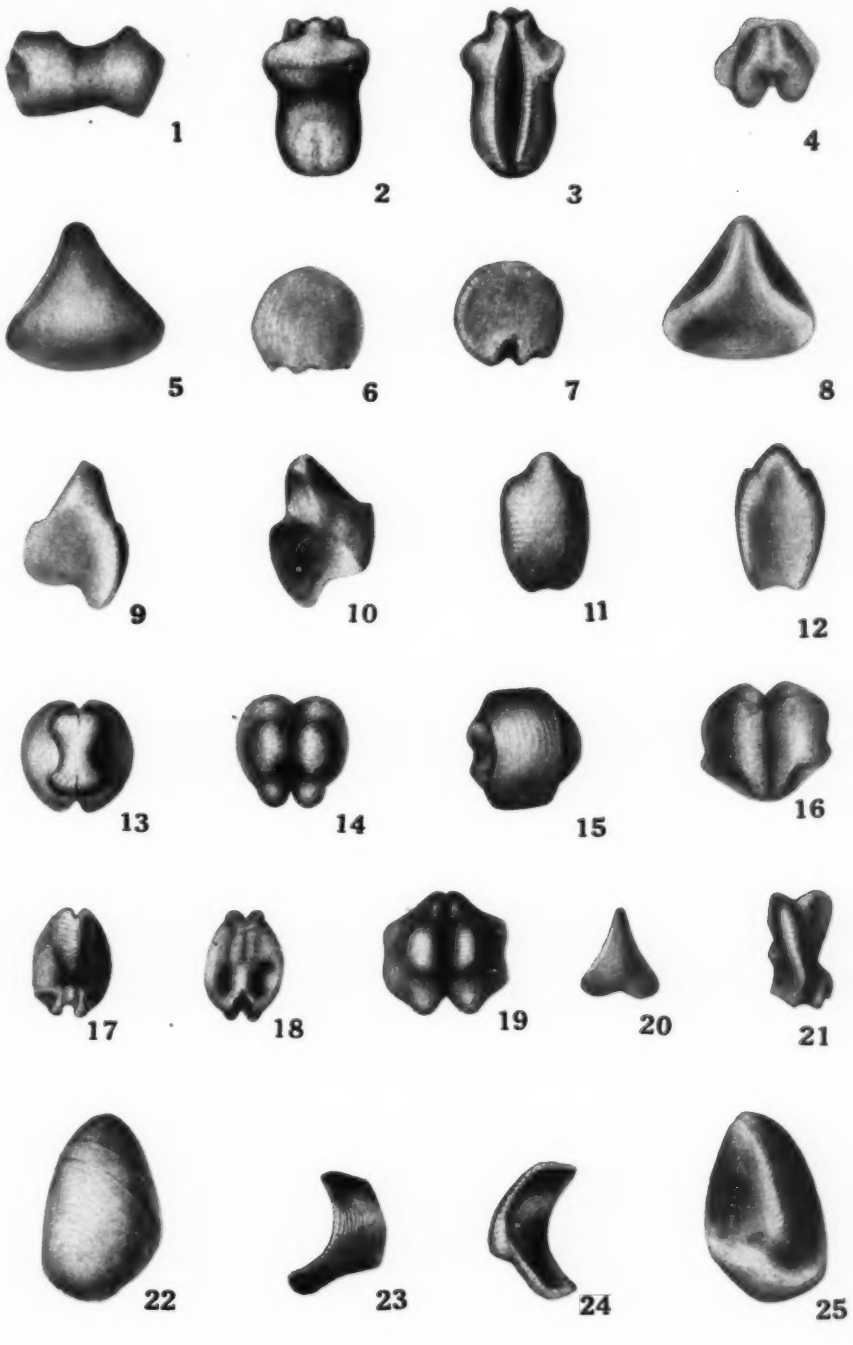
This species is composed of plates D, G, K, O, and S. The generic name *Dolicharthra*, meaning long joint, has been chosen with reference to the vertebral ossicle D. The specific name is derived from the town of Bemelen, South Limburg, Holland, near which most of the plates belonging to this species were found.

Radial shield S.—(Pl. 16, figs. 6, 7.) Outline semicircular, straight edge aboral. Outer (dorsal) surface irregularly flat; inner (ventral) surface smooth except in center of aboral margin, where there is a deep pit surrounded by a slightly raised articulation area. Plate is thinner near adoral margin than at

EXPLANATION OF PLATE 16

FIGS. *1–12—Dolicharthra bemelenica* C. Berry, n. gen. and n. sp. *1–4*, Lateral, dorsal, ventral, and adoral views of vertebral ossicle D. *5, 8*, Dorsal and ventral views of dorsal arm plate G. *6, 7*, Dorsal and ventral views of radial shield S. *9. 10*, Outside and inside views of lateral arm plate O. *11, 12*, Ventral and dorsal views of ventral arm plate K. *13–16, 19, 22–25—Asteronyx valkenburgensis* C. Berry, n. sp. *13–16, 19*, Adoral, aboral, lateral, dorsal and ventral views of vertebral ossicle C. *22, 25*, Outside and inside views of radial shield T. *23, 24*, Outside and inside views of lateral arm plate N. *17, 18, 20, 21*—Genus and species undetermined. *17, 18, 21*, Views of same vertebral ossicle. *20*, Dorsal view of dorsal arm plate.

All figures approximately ×14.



C. Berry, Senonian Ophiurans

UNIV. OF MICH.

aboral margin. Length, 1.04 mm.; width, 1.12 mm.; thickness, 0.32 mm.

Dorsal arm plate G.–(Pl. 16, figs. 5, 8.) Outline triangular with sides concave. Outer (dorsal) surface slightly swollen; adoral apex sharply pointed, lateral margins evenly concave; aboral end irregular, slightly concave, aboral-lateral corners rounded; inner (ventral) surface slightly concave, greatest concavity in aboral part. Length, 1.12 mm.; width across aboral end, 0.4 mm.

Ventral arm plate K.—(Pl. 16, figs. 11, 12.) Outline modified rectangle, aboral margin straight, adoral margin having a medial equilateral triangular projection, lateral margins (longest sides) evenly convex. Outer (ventral) surface swollen, sloping gently to aboral margin; inner (dorsal) surface slightly concave; adoral end of the plate thick, aboral thin. Width, 0.88 mm.; length, 1.36 mm.

Lateral arm plate O.—(Pl. 16, figs. 9, 10.) Outline irregular; right side (viewed from the outside) straight, offset in center, curving down to ventral rounded end; middle portion of left side occupied by large convex projection. Right edge thin, left edge thick. Outer surface smooth, flat except along right margin, where it suddenly descends steeply to margin of plate; inner surface concave. Height, 1.36 mm.; width, 1.04 mm.

Vertebral ossicle D.—(Pl. 16, figs. 1–4.) Adoral view: Outline triangular, apex dorsal, ventral side indented by deep V-shaped lower canal furrow. Surface rounding down to margin; dorsal apex indented by shallow groove; surface uneven, showing no outstanding types of grooves or ridges for articulating.

Aboral view: Outline oval; deep V-shaped lower canal furrow indenting ventral side; shallow groove indenting dorsal side. Surface uneven, rounding down to margin of plate; center occupied by steep-sided raised X-shaped area, whose lower limb flanks side of lower canal furrow and whose upper limbs are united in a solid mass.

Lateral view: Outline irregular; dorsal and ventral sides concave, the dorsal the more concave; adoral and aboral ends varyingly rounded; all corners rounded. Surface uneven, concave medially, rounding gently down to dorsal margin; raised rounded area near aboral end, aboral of which is deep depression along entire aboral end of plate.

Dorsal view: Outline irregular; adoral end rounded, slightly depressed at margin; lateral sides concave in middle; aboral end having rounded projection in middle. Surface rounded, aboral part elevated, central part depressed, adoral part raised but not as much as aboral part. Surface covered with foreign matter.

Ventral view: Outline same as in reverse view. Surface practically flat, with deep steep-sided lower canal furrow running entire length of plate. This groove is deeper and wider in central part and is flanked by two raised areas at adoral end of plate. Length, 1.48 mm.; width, 1.04 mm.; height, 0.72 mm.

GENUS AND SPECIES UNDET.

Plate 14, figures 11, 12; plate 15, figures 15, 16, 18–21, 23, 24; plate 16, figures 17, 18, 20, 21.

Several miscellaneous plates whose identification is uncertain have been figured, but not described. Each kind is represented in the collection by only one specimen.

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UPPER CAMBRIAN FAUNAS OF THE CAP MOUNTAIN FORMATION OF TEXAS

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ABSTRACT

Three early Upper Cambrian faunas—the *Cedaria*, *Crepicephalus* and *Aphelaspis*—occur in the Cap Mountain formation of Texas. Preliminary faunal lists for each are given, and the relation of the faunal sequence to the recognized stratigraphic units of the region is discussed. Several new genera and species are described.

This paper presents a preliminary report on the faunas in the Upper Cambrian Cap Mountain formation of central Texas and describes several of the more important new genera and species. The field work for this problem was financed by a grant in aid from the National Research Council.

The Cap Mountain formation, originally described by Sidney Paige in 1912 (1), consists of 220 feet of gray crystalline limestone overlain by a persistent 30-foot sandstone member. The basal beds of the Cap Mountain are markedly arenaceous and grade downward into the Hickory sandstone. The crystalline limestone constituting the greater part of the formation is characterized throughout its thickness by varying amounts of glauconite. Approximately 200 feet above the base are greensands intercalated with very fossiliferous limestone lenses. Through the succeeding 20 feet the limestone lenses dwindle in size and thickness until the beds are composed entirely of the barren greensands of the Lion Mountain sandstone member. The Cap Mountain, as here delineated, carries the *Cedaria*, *Crepicephalus*, and *Aphelaspis* faunas and is the equivalent of the Eau Claire member of the Dresbach formation of Wisconsin. The faunal break between the Dresbach and the Franconia occurs in the Texas section at the horizon of the barren sands of the Lion Mountain sandstone member. The upper beds of these greensands pass by the gradual increase of the lime content directly into the limestones of the Wilberns formation. The boundary between the Cap Mountain and the Wilberns, drawn arbitrarily at the first occurrence of the *Camaraspis* fauna, falls within these transition beds.

The known occurrences of the *Cedaria* fauna reveal the gradations of the basal part of the Cap Mountain. In the section on Potatotop Hill, Burnet County, species belonging to this fauna appear in beds of the Hickory sandstone 100 feet below the summit of the hill. Near the top of the section other species of this fauna occur in sandy calcareous

beds, which are arbitrarily regarded as the base of the Cap Mountain because of the high lime content. Five miles south, on the southwest side of Lion Mountain, Burnet County, a large *Cedaria* fauna has been obtained from the basal 110 feet of the Cap Mountain. Specimens of this fauna collected 110 feet above the recognized base in this section must represent nearly the top of the *Cedaria* zone, as the collection made 15 feet higher stratigraphically belongs to the *Crepicephalus* fauna. The following species have been identified from the *Cedaria* zone:

Cedaria burnetensis (Walcott)
Tricrepicephalus texanus (Shumard)
Norwoodia tenera Walcott
Deiracephalus aster (Walcott)
Millardia avitas Walcott
Millardia magnagranulata Lochman, n. sp.
Kingstonia texana Lochman, n. sp.
Meteoraspis bipunctata Lochman, n. sp.
Coosia sp.
Coosella sp.
Agnostus sp.
Acrotreta sp.

The *Crepicephalus* fauna occupies a zone averaging 60 feet in thickness through the middle part of the formation. The fossils are abundant throughout the zone at many widely separated localities. The following species have been recognized from this horizon:

Crepicephalus auratus Lochman, n. sp.
Crepicephalus sp. undet. 1
Crepicephalus sp. undet. 2
Tricrepicephalus cf. *T. dis* (Walcott)
Llanoaspis modesta Lochman, n. gen., n. sp.
Llanoaspis undulata Lochman, n. sp.
Kingstonia pontotocensis Lochman, n. sp.
Pemphigaspis inexpectans Lochman, n. sp.
?*Meteoraspis motra* (Walcott)
Coosia sp.
Coosella sp.
Two genera of agnostian trilobites
Billingsella sp.

The *Aphelaspis* zone, approximately 35 feet thick, immediately overlies the *Crepicephalus*. In the section on Morgan Creek the fauna appears first rather sparsely in glauconitic light-gray limestones that are similar lithologically to, and apparently perfectly conformable with, the preceding *Crepicephalus* beds. The same species continue upward into the limestone lenses of the succeeding arenaceous beds. The lenses of these upper strata are crowded with the cranidia and pygidia of five species of *Aphelaspis* and the valves of *Lingulella arguta* (Walcott). The trilobites disappear with the last thin limestone lenses, but the brachiopod continues several feet higher, forming calcareous patches in the greensands. The following species occur in this fauna:

Aphelaspis depressa (Shumard)
Aphelaspis 4 n. sp.
Pseudolisania texana Lochman, n. sp.
Pseudolisania raaschi Lochman, n. sp.
Raaschella ornata Lochman, n. gen., n. sp.
Blountia sp.
Agnostus sp.
Lingulella arguta (Walcott)
Lingulepis sp.
Acrotreta sp.

The five most complete sections in the eastern part of the Central Min-

eral Region have been plotted to scale in figure 1 to show the succession of faunas as it occurs in the lower part of the Upper Cambrian in this region and to illustrate the relation of the faunal sequence to the stratigraphic units. Several more approximately complete sections are known in the northern and western areas of this region, but as all the collections from these sections have not yet been studied, they are not included in the present paper. The detailed collecting done in connection with this problem has shown conclusively that these early Upper Cambrian formations are even more extensively faulted than was hitherto believed, and at most localities the section is too disturbed to give either an accurate thickness for the formations or a complete faunal succession. The persistent Lion Mountain sandstone member was found to be the best datum plane from which to take measurements.

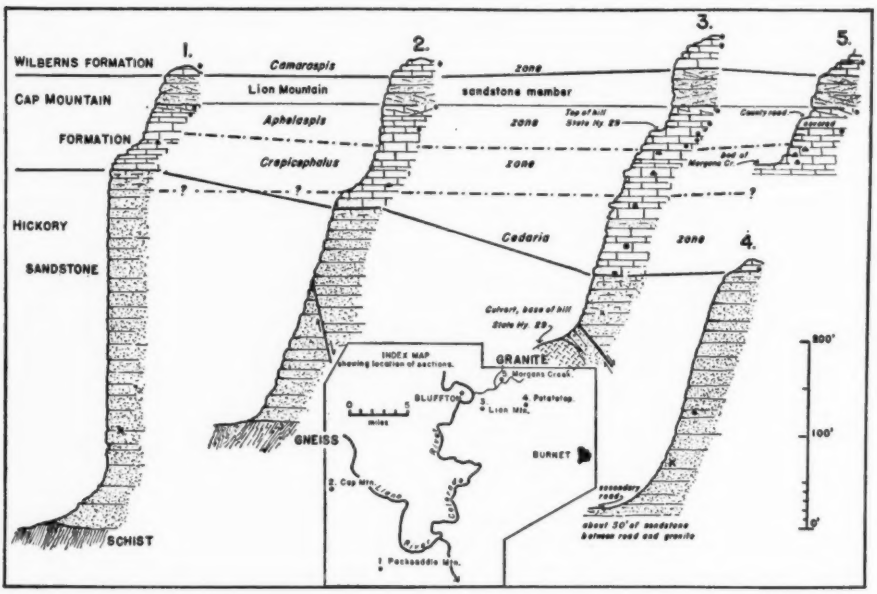


FIG. 1—Sec. *1*, Packsaddle Mountain, south end of the west peak; sec. *2*, Cap Mountain, east face of east peak; sec. *3*, Lion Mountain, southwest side, along Highway 29 for the first 225 feet, then up the face of butte just north of highway; sec. *4*, Potatotop Hill, west face; sec. *5*, South face of point between North and South Forks of Morgan Creek. Exact horizon of collections marked by symbols. Collections marked × in secs. *1*, *3*, and *4* consist entirely of oboloid brachiopods unplaced in any of the trilobite faunas. Note the check between the total thickness of the two units in sec. *1* and the thickness for the same units from the combined secs. *3* and *4*.

The Lion Mountain section (section 3, fig. 1) contains the greatest thickness and fullest development of the Cap Mountain formation in the eastern area and is the only section in the area from which a complete

faunal sequence has been obtained to date. It is quite probable that future field work will show the Morgan Creek section (section 5) to be comparable in thickness and completeness of faunal zones to that of Lion Mountain, as outcrops of the Cap Mountain continue in the river bed for half a mile downstream from the locality at which the section was measured. The gradual thinning of the Cap Mountain to the south of this section is the most striking feature brought out by figure 1. This fact is especially important as it coincides with the pronounced thickening of the Hickory sandstone in the Packsaddle section (section 1) and the disappearance of the *Cedaria* fauna from the basal limestones of the Cap Mountain in sections 1 and 2. These conditions definitely suggest that the basal 110 feet of the Cap Mountain formation as developed in the Lion Mountain section is gradually replaced to the south by an increased thickness of Hickory sandstone, and that, in the southern sections, the *Cedaria* fauna is to be sought in the Hickory rather than in the Cap Mountain. The presence of this fauna in sandstones and very arenaceous limestones in sections 3 and 4 demonstrates the ability of the fauna to live in both environments. In all probability, it will be found as well developed in the south as in the north when the correct stratigraphic horizon has been examined. The interpretation offered here of these sections recognizes the Cap Mountain formation and the Hickory sandstone as merely lithologic terms for an intergrading sequence, which is everywhere strictly conformable.

SYSTEMATIC DESCRIPTIONS

Order OPISTHOPARIA Beecher
Family CREPICEPHALIDAE Kobayashi

CREPICEPHALUS AURATUS Lochman, n. sp.

Plate 17, figures 15–18

Cranidium short and broad with a moderately convex, broadly conical glabella; occipital furrow narrow, well defined; occipital ring of medium width, flat with a small median node; dorsal furrow narrow, completely outlining glabella. Fixed cheeks one-third width of glabella, slightly convex; palpebral lobe large, crescentiform, equal to one-half the length of glabella; palpebral furrow narrow, deep; ocular ridge faint; frontal limb of medium width, convex, sloping to the deep, narrow transverse furrow; frontal border narrow, convex, rimlike; anterior margin rounded. Posterolateral limbs narrow with a narrow, well-defined intramarginal furrow. Free cheek narrow, elongate, with large eye at inner angle; ocular platform narrow, slightly convex; marginal furrow narrow, shallow; marginal border of medium width, flat, with a pointed anterior projection and a long slender genal spine. Facial suture cutting anterior margin a short distance out from center of cranidium, curving outward to transverse furrow and thence running straight back to palpebral lobe. Hypostoma oval in outline with short lappets; anterior lobe oval, tumid; posterior lobe semicircular in outline, convex; lateral and posterior margins narrow, rimlike; two pairs of deep lateral pits, one pair between anterior and posterior lobes and other pair between posterior lobe and posterior margin.

Pygidium short, transverse; axial lobe wide, convex, extending nearly to posterior margin, divided by narrow shallow furrows into four segments and a terminal part; pleural lobes narrower than axial, flat, divided into four segments by broad shallow furrows, which curve backward into the bases of the spines; marginal border narrow, widest at posterolateral corners; two short, rounded slender spines which curve outward and backward from the pygidium. Inner surface of test minutely punctate. Dimensions of cranidium, 4.5×5.5 mm. Dimensions of pygidium, 2×3.25 mm.

The several cranidia, hypostoma, one pygidium, and some of the free cheeks that are assigned to this species are from a single locality. Their small size suggests that they do not represent adult individuals. The more common *Crepicephalus* species of this fauna is represented by the pygidia described under *Crepicephalus* sp. undet. 1.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Holotype (a cranidium, U. S. Nat. Mus. 95509) and three paratypes (an immature cranidium, a hypostoma, and a pygidium, U. S. Nat. Mus. 95510) from outcrops along east road at Fredonia, San Saba County, Tex. Paratype (a free cheek, U. S. Nat. Mus. 95511) from southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

CREPICEPHALUS sp. undet. 1
Plate 17, figures 19–22

Pygidium transverse, with two short spines; axial lobe wide, convex, with broadly rounded posterior extremity, and extending nearly full length of pygidium; divided into five segments and a terminal part by shallow furrows; pleural lobes same width as axial, flat, sloping down to moderately wide marginal border; divided into three segments by broad shallow furrows; posterior spines short and flat, extending directly backward from the marginal border; posterior margin straight. Inner surface coarsely punctate.

The species of *Crepicephalus* to which this pygidium belongs is a very common member of the faunal assemblage, for the pygidia are known from many localities. However, as no cranidia can yet be associated with the pygidia, the species is not named. The pygidia range in size from 2.25×4 mm. to 11×20 mm. Although none has been found as small as that of *C. auratus*, it is considered unlikely that the characteristics should have changed so radically within such a short growth period.

The pygidium of *Crepicephalus* sp. undet. 1 differs from that of *C. auratus* in the wider marginal border unmarked by pleural segments, the greater width of the pleural lobes, and the straight posterior direction of the spines.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Figured pygidia (U. S. Nat. Mus. 95018) from outcrop in bed of South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

CREPICEPHALUS sp. undet. 2
Plate 17, figure 23

Pygidium subquadrate in outline, with two very short, tapered spines; axial lobe wide, markedly convex, extending two-thirds the length of pygidium, and divided into three segments and a broad terminal part by wide shallow furrows; pleural lobes narrower than axial, flat, sloping gently to the broad flat marginal border; divided into two wide segments by broad furrows; posterior spines short, flat, broad at bases and tapering rapidly to a point; posterior margin curved.

This type of pygidium represents a third species of *Crepicephalus* in this fauna from the Cap Mountain, but as no cranidium that can be definitely associated with it has been found it is not described specifically. Although quite distinctive from the two other types of

pygidia here described, it is very similar to an undescribed species from the Upper Cambrian of Wisconsin.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Figured pygidium (U. S. Nat. Mus. 95515) from outcrop along road to Cherokee, 5 miles northeast of Pontotoc, San Saba County, Tex.

Family PLETHOPELTIDAE Raymond

KINGSTONIA PONTOTOCENSIS Lochman, n. sp.
Plate 18, figures 14–16

Cranidium 3 mm. in length with a convexity of 1.25 mm.; greatest convexity anterior to transverse median line; glabella wide, subquadrate, curving down abruptly at anterior end; shallow occipital furrow and narrow occipital ring on inner surface of test; dorsal furrow outlining glabella on inner surface, deeply impressed posteriorly; outer surface of test smooth. Fixed cheeks moderately wide, nearly vertical; palpebral lobes very small; frontal limb of medium width, vertical; transverse furrow narrow, shallow and straight, delimiting a very narrow, flat, vertical frontal border. Posterolateral limbs broad and short, no intramarginal furrow. Facial suture cutting anterior margin lateral to dorsal furrow, curving back to and around the palpebral lobes, and thence curving abruptly backward to cut posterior margin. Free cheek, thorax, and pygidium not known.

This species differs from *K. texana* in the abrupt anterior change in convexity of the cranidium and the much shorter, wider posterolateral limbs. It is one of the less common forms of the *Crepicephalus* fauna.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Holotype (a cranidium, U. S. Nat. Mus. 95512) from outcrop in bed of South Fork of Morgan Creek, 4.2 miles northwest of Highway 29, Burnet County, Tex.

KINGSTONIA TEXANA Lochman, n. sp.
Plate 18, figures 20–24

Cranidium small, 3 mm. in length, moderately and regularly convex; glabella subquadrate, rounded in front and moderately convex; no occipital ring or furrow on outer surface; faint traces of a dorsal furrow along the posterior sides of glabella. Fixed cheeks moderately wide, sloping down steeply; palpebral lobes very small; frontal limb medium-sized, steeply sloping; transverse furrow narrow, straight and well defined; narrow vertical frontal border marked by microscopic longitudinal ridges. Posterolateral limbs of medium size, no intramarginal furrow. Facial suture cutting anterior margin on line with center of fixed cheeks, passing outward in a flat curve to and a round palpebral lobe; thence curving outward and backward to cut posterior margin just within genal angle.

Pygidium triangular; axial lobe of medium width, low, smooth on outer surface; faint trace of dorsal furrow along anterior sides; pleural lobes same width as axial, flat, smooth; marginal border vertical, narrow at sides but increasing in width at posterior edge.

This species differs from *K. apion* in the curvature of the anterior part of the facial suture and the very small palpebral lobes. It is a common member of the *Cedaria* fauna.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Holotype (a cranidium, U. S. Nat. Mus. 95513) and paratypes (a cranidium and a pygidium, U. S. Nat. Mus. 95514) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

Family PAGODIDAE Kobayashi

PSEUDOLISANIA RAASCHI Lochman, n. sp.
Plate 18, figures 25–34

Cranidium subquadrate in outline, glabella subquadrate, long and narrow,

moderately convex with a narrow median ridge; four pairs of short shallow glabellar furrows; occipital furrow forming deep broad pits at sides and obsolete in middle; occipital ring of medium width; dorsal furrow broad and shallow. Fixed cheeks one-half width of glabella; palpebral lobes small; ocular ridge narrow, elevated; frontal border of medium width, slightly concave; anterior margin rounded. Posterolateral limbs broad, with a broad shallow intramarginal furrow. Facial suture cutting anterior margin on a line with dorsal furrow. Hypostoma subquadrate, with a narrow raised anterior margin and short blunt lappets; anterior lobe oval, tumid; posterior lobe convex, semicircular; two pairs of lateral pits.

Pygidium semicircular; axial lobe of medium width, convex, tapering posteriorly, divided into eight segments and a small terminal part by broad shallow furrows; pleural lobes same width as axial, slightly convex, divided into eight segments by shallow furrows, which fade out on the moderately wide, concave marginal border. Outer surface of test smooth.

This species is a striking but not

EXPLANATION OF PLATE 17

All figures natural size except as otherwise noted. All specimens figured are in the U. S. National Museum and are from the Cap Mountain formation.

FIGS. *1–3*—*Meteoraspis metra* (Walcott). Dorsal, front and profile views of genoholotype, a fragmentary cranidium, ×2, U. S. Nat. Mus. 23858. Zone unknown. Potatotop Hill, 6 miles northwest of Burnet, Burnet County, Tex.

4–8—*Meteoraspis bipunctata* Lochman, n. sp. *6, 7, 8*, Dorsal, front, and profile views of holotype, a perfect cranidium, ×2, U. S. Nat. Mus. 95526. *4, 5*, Paratype, dorsal, and front views of larger cranidium, ×2, U. S. Nat. Mus. 95527. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County. Tex.

9–14—*Llanoaspis modesta* Lochman, n. gen. and n. sp. *10, 14*, Dorsal and front views of holotype, a perfect cranidium, ×3, U. S. Nat. Mus. 95520. *9*, Paratype, a large cranidium, ×3, U. S. Nat. Mus. 95521. *11, 12, 13*, Paratype, rear, profile and dorsal views of nearly perfect pygidium, ×3, U. S. Nat. Mus. 95521. *Crepicephalus* zone, outcrop along the east road at Fredonia, San Saba County, Tex.

15–18—*Crepicephalus auratus* Lochman, n. sp. *15*, Dorsal view of holotype, a fragmentary cranidium, ×5, U. S. Nat. Mus. 95509. *17*, Paratype, an immature cranidium, ×5, U. S. Nat. Mus. 95510. *18*, Paratype, a small pygidium without posterior spines, ×5, U. S. Nat. Mus. 95510. *Crepicephalus* zone, outcrop along east road at Fredonia, San Saba County, Tex. *16*, Paratype, a perfect free cheek, ×5, U. S. Nat. Mus. 93011. *Crepicephalus* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

19–22—*Crepicephalus* sp. undet. 1. *19, 20, 21*, Dorsal, rear, and profile views of small pygidium, ×5, U. S. Nat. Mus. 95018. *22*, Dorsal view of large pygidium preserving some of outer surface of test, U. S. Nat. Mus. 95018. *Crepicephalus* zone, outcrop in bed of South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

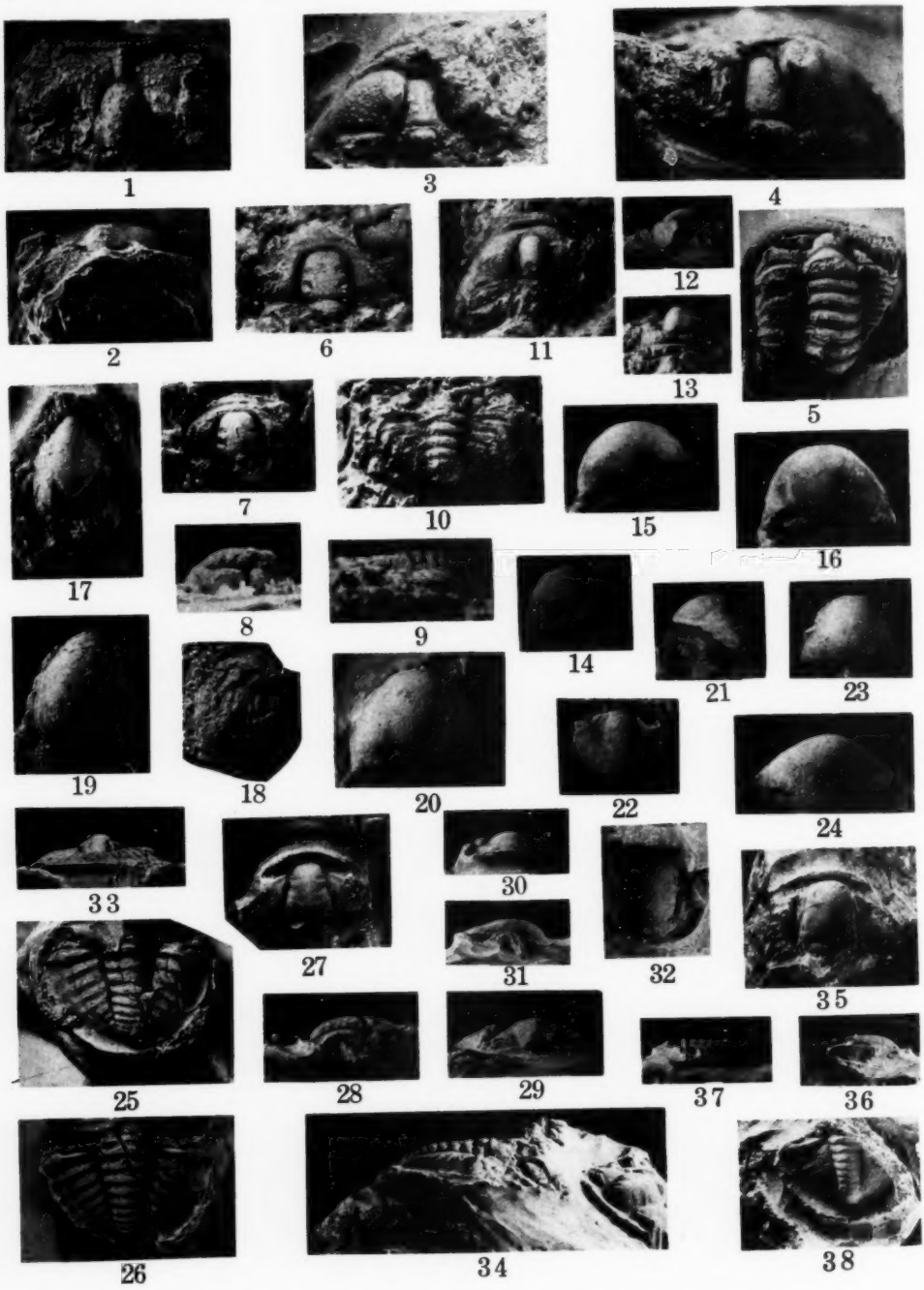
23—*Crepicephalus* sp. undet. 2. Cast of a small, nearly perfect pygidium, ×5, U. S. Nat. Mus. 95515. *Crepicephalus* zone, outcrop along road to Cherokee, 5 miles northeast of Pontotoc, San Saba County, Tex.

24–26—*Llanoaspis undulata* Lochman, n. sp. *24*, Dorsal view of holotype, a cranidium lacking posterolateral limbs, ×3, U. S. Nat. Mus. 95522. *25*, Paratype, a large cranidium, ×3, U. S. Nat. Mus. 92023. *26*, Paratype, a fragmentary pygidium, ×3, U. S. Nat. Mus. 95523. *Crepicephalus* zone, at cross roads half a mile west of Cherokee, San Saba County, Tex.

27, 28—*Pemphigaspis inexpectans* Lochman, n. sp. Dorsal and front views of holotype, ×5, U. S. Nat. Mus. 95016. *Crepicephalus* zone, outcrop in bed of South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

29—*Cedaria burnetensis* (Walcott). Dorsal view of holotype, a cranidium with one posterolateral limb missing, preserved in friable sandstone, ×3, U. S. Nat. Mus. 23854. *Cedaria* zone, Potatotop Hill, 6 miles northwest of Burnet, Burnet County, Tex. (U. S. Nat. Mus. loc. 67-a).

Lochman, Upper Cambrian Trilobites



Lochman, Upper Cambrian Trilobites and Brachiopods

abundant member of the *Aphelaspis* fauna. Basing measurements on the size of the hypostome figured, the complete adult carapace must have been between 5 and 6 inches in length.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Aphelaspis* zone). Holotype, (a cranidium) and paratype (a pygidium on a single piece of rock, U. S. Nat. Mus. 95516) from outcrops along road 2.1 miles east of Cherokee, San Saba County, Tex. Paratype (hypostoma, U. S. Nat. Mus. 95517) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

EXPLANATION OF PLATE 18

All figures natural size except as otherwise noted. All specimens are from the Cap Mountain formation.

FIGS. *1, 2*—*Deiracephalus aster* (Walcott). Dorsal and front views of only specimen obtained, ×3, Mount Holyoke Mus. 654. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

3—*Millardia magnagranulata* Lochman, n. sp. Dorsal view of holotype, an imperfect cranidium, ×3, U. S. Nat. Mus. 95015. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

4, 5—*Millardia avitas* Walcott. *4*, Dorsal view of a large imperfect cranidium, ×3, Mount Holyoke Mus. 655. *5*, Anterior portion of a thorax, ×3, Mount Holyoke Mus. 656. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

6–10—*Raaschella ornata* Lochman, n. gen. and n. sp. *6*, Dorsal view of holotype, ×5, U. S. Nat. Mus. 95524. *7, 8*, Dorsal and profile views of paratype, an incomplete cranidium, ×5, U. S. Nat. Mus. 95525. *9, 10*, Profile and dorsal views of paratype, a pygidium, ×5, U. S. Nat. Mus. 95525. *Aphelaspis* zone, outcrop along Mill Creek road 2 miles south of Mason, Mason County, Tex.

11–13—*Norwoodia tenera* Walcott. Dorsal, profile, and front views of a nearly perfect cranidium, ×5, Mount Holyoke Mus. 657. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

14–16—*Kingstonia pontotocensis* Lochman, n. sp. *14, 15*, Profile and dorsal views of holotype, ×5, U. S. Nat. Mus. 95512. *16*, Dorsal view of holotype taken with reflected light showing the dorsal and occipital furrows on the inner surface. *Crepicephalus* zone, outcrop in bed of South Fork of Morgan Creek, 4.2 miles northwest of Highway 29, Burnet County, Texas.

17–19—*Lingulella arguta* (Walcott). *17*, Ventral valve showing exterior, ×2, U. S. Nat. Mus. 95017. *18*, Dorsal valve showing internal markings, ×2, U. S. Nat. Mus. 95017. *19*, Ventral valve, some of internal markings showing through inner shell lamellae, ×2, U. S. Nat. Mus. 95017. *Aphelaspis* zone, outcrop on road along South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

20–24—*Kingstonia texana* Lochman, n. sp. *20, 21, 24*, Dorsal, profile, and front views of holotype, a perfect cranidium, ×5, U. S. Nat. Mus. 95513. *23*, Paratype, a smaller cranidium, ×5, U. S. Nat. Mus. 95514. *22*, Paratype, a small pygidium, ×5, U. S. Nat. Mus. 95514. *Cedaria* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

25–34—*Pseudolisania raaschi* Lochman, n. sp. *27, 28, 29*, Dorsal, profile, and front views of holotype, a nearly perfect cranidium, U. S. Nat. Mus. 95516. *25, 26, 33*, Cast, dorsal, and rear views of paratype, a pygidium, U. S. Nat. Mus. 95516. *34*, Association of holotype and paratype. *Aphelaspis* zone, along road 2.1 miles east of Cherokee, San Saba County, Tex. *30, 31, 32*, Front, profile, and ventral views of a large hypostoma, paratype, U. S. Nat. Mus. 95517. *Aphelaspis* zone, southwest side of Lion Mountain on Highway 29, 9 miles northwest of Burnet, Burnet County, Tex.

35–38—*Pseudolisania texana* Lochman, n. sp. *35, 36*, Dorsal and profile views of holotype, an imperfect cranidium, U. S. Nat. Mus. 95518. *Aphelaspis* zone, outcrop on road along South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex. *37, 38*, Profile and dorsal views of paratype, a broken pygidium, U. S. Nat. Mus. 95519. *Aphelaspis* zone, along road 2 miles southwest of Cherokee, San Saba County, Tex.

PSEUDOLISANIA TEXANA
Lochman, n. sp.
Plate 18, figures 35–38

Cranidium with a broad subquadrate moderately convex glabella; two pairs of faint glabellar furrows; occipital furrow shallow, present only at sides; occipital ring narrow, flat; dorsal furrow narrow, shallow. Fixed cheeks one-third width of glabella, flat; palpebral lobes small; ocular ridge wide and prominent; frontal border narrow, flat, marked by three transverse parallel lines; anterior margin rounded. Posterolateral limbs wide, moderately long; intramarginal furrow broad and shallow. Facial suture cutting anterior margin near the sides of cranidium.

Pygidium semicircular; axial lobe narrow, moderately convex, with bluntly rounded posterior extremity, divided into eight segments and a terminal part by narrow shallow furrows; pleural lobes wider than axial, flat, divided into seven segments by faint narrow furrows; a narrow concave marginal border.

This species is quite close to *Pseudolisania breviloba* (Walcott) from theNolichucky limestone of Tennessee. It is also a persistent but not abundant member of the *Aphelaspis* fauna.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Aphelaspis* zone). Holotype (a cranidium, U. S. Nat. Mus. 95518) from outcrop along road at South Fork of Morgan Creek, 4.2 miles northwest of Highway 29, Burnet County, Tex. Paratype (a pygidium, U. S. Nat. Mus. 95519) from outcrops along road 2 miles southwest of Cherokee, San Saba County, Tex.

INCERTAE SEDIS

LLANOASPIS Lochman, n. gen.

Cranidium square in outline; glabella elongate, convex; three pairs of short glabellar furrows, posterior pair arcuate; occipital furrow broad and deep; occipital ring narrow, slightly convex; dorsal furrow narrow, outlining glabella. Fixed cheeks wide, elevated; palpebral lobes small, flaplike, situated posterior to the transverse median line of glabella; a narrow shallow palpebral furrow; ocular ridge prominent, crossing fixed cheeks diagonally to dorsal furrow slightly anterior to middle of glabella; no frontal limb; transverse furrow narrow and deep, on line with front of glabella; frontal border wide; anterior margin bluntly pointed. Posterolateral limbs long, narrow below eyes and expanding rapidly to margin; intramarginal furrow deep, narrow, turning forward before reaching lateral margin. Facial suture cutting anterior margin near center of cranidium, curving backward and outward to transverse furrow and then straight back to palpebral lobe around which it passes; thence running forward and outward to marginal furrow, beyond which it curves down and back to cut posterior margin within genal angle. Hypostoma subcircular in outline, with straight anterior margin; no lappets; oval central lobe slightly convex, sloping evenly into wide flat marginal border; two parallel pairs of pits along sides of central lobe.

Pygidium transverse and convex; axial lobe convex, narrow, extending practically full length of pygidium, divided into six or more segments and a terminal part by narrow shallow furrows; pleural lobes wide, convex, divided by broad shallow furrows into six segments, which continue outward onto the marginal border; border widest at the anterior, narrowing posteriorly to a thin rim below axial lobe, and changing in profile from concave to convex; outer edge sinuous.

Genotype: *Llanoaspis modesta* Lochman, n. sp.

This peculiar genus is common in the *Crepicephalus* zone of the Cap Mountain. The course of the intramarginal furrow suggests a proparian form. However, although the free cheek has not yet been found, the author, after careful study of the course of the facial suture on all the available cranidia, has come to the conclusion that the genus is one of those unusual opisthoparian forms

(such as *Cedaria* and *Damesella*) in which the facial suture nearly reaches the lateral margin before turning inward and backward to cut the posterior margin, leaving the genal angle on the free cheek.

LLANOASPIS MODESTA
Lochman, n. sp.
Plate 17, figures 9–14

Cranidium with an elongate, convex, subquadrate glabella, rounded in front; glabellar furrows faint; dorsal furrow deep and narrow. Fixed cheeks slightly more than one-half width of glabella, convex and elevated; palpebral lobes small, crescentiform; ocular ridge well defined; transverse furrow narrow, well defined in front of fixed cheeks; frontal border wide, flat, sloping slightly downward from transverse furrow. Posterolateral limbs long, broad at outer margin; intramarginal furrow deep, narrow. Facial suture cutting anterior margin near center of cranidium.

Pygidium very convex; axial lobe narrow, long, tapering posteriorly; six segments and a long terminal section marked off by narrow shallow furrows; pleural lobes wide, divided by broad furrows into six segments, which curve backward sharply onto the marginal border; border varying in width and undulating along the edge. Outer surface of test smooth.

This species is distinguished by the wide flat frontal border of the cranidium. Specimens of the cranidium range from 2 to 8 mm. in length.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Holotype (a cranidium, U. S. Nat. Mus. 95520) and paratypes (a pygidium and a cranidium, U. S. Nat. Mus. 95521) from outcrop along the east road at Fredonia, San Saba County, Tex.

LLANOASPIS UNDULATA
Lochman, n. sp.
Plate 17, figures 24–26

Cranidium quadrate with a convex, broadly conical glabella; arcuate posterior pair of glabellar furrows deeply impressed; occipital furrow deep at sides, shallow at median line; dorsal furrow deep, narrow. Fixed cheeks one-half width of glabella, flat and sharply elevated; palpebral lobes small, crescentiform; palpebral furrow very narrow; ocular ridge narrow, prominent; transverse furrow narrow, deep, and straight; frontal border wide, undulating—convex in front of transverse furrow, then concave, and then sharply upturned at the front. Posterolateral limbs long, expanding rapidly near margin; intramarginal furrow narrow, well defined. Facial suture cutting anterior margin near center of cranidium. Hypostoma subcircular in outline with a low oval central lobe, a flat marginal border of medium width, and two pairs of lateral pits.

Pygidium transverse, convex; axial lobe narrow, convex, extending nearly full length of pygidium, with posterior extremity bluntly rounded; pleural lobes wide, very convex, divided into seven segments by shallow furrows; marginal border of varying width with a sinuous outer edge. Outer surface of test smooth.

This species is more common than *Llanoaspis modesta* in the *Crepicephalus* fauna and occurs at a number of localities. It is distinguished by the undulating frontal border. Cranidia range from 5 to 8 mm. in length.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Holotype (a cranidium, U. S. Nat. Mus. 95522) and paratypes (a cranidium, a pygidium, and a hypostoma, U. S. Nat. Mus. 95523) from outcrops at cross roads half a mile west of Cherokee, San Saba County, Tex.

RAASCHELLA Lochman, n. gen.

Cranidium short and wide, with a strongly convex, broadly conical glabella; two pairs of glabellar furrows, posterior pair arcuate; occipital furrow deep and narrow; occipital ring convex, broad at median line and narrowing at sides; dorsal furrow broad, outlining glabella. Fixed cheeks narrow, slightly convex;

palpebral lobes small, narrow, situated on transverse median line of cranidium; palpebral furrow very narrow; ocular ridge narrow and faint; frontal limb narrow, convex; transverse furrow narrow and shallow; frontal border narrow, slightly convex; anterior margin rounded. Posterolateral limbs long, moderately wide, marked by a broad intramarginal furrow. Free cheek narrow, elongate, with a narrow convex marginal border and a narrow but well-defined marginal furrow; small eye situated at inner angle; a short pointed anterior projection and a rounded genal angle. Facial suture cutting anterior margin near center of cranidium, curving evenly outward and backward to palpebral lobes around which it passes; thence running straight outward and curving backward to cut posterior margin.

Pygidium subtriangular in outline; axial lobe moderately convex, narrow, extending nearly to posterior margin, and divided by broad shallow furrows into four or five segments and a terminal part; pleural lobes wider than axial, flat, and divided by faint furrows into four or more segments, which turn abruptly backward and downward near the outer margin; marginal border extremely narrow, rimlike.

Genotype: *Raaschella ornata* Lochman, n. sp.

The genus is named in honor of Mr. Gilbert O. Raasch, who first recognized the form in the *Aphelaspis* fauna of the Wisconsin section and has very kindly given the author permission to describe it.

This small genus appears to be as diagnostic of the *Aphelaspis* zone as the genus *Aphelaspis* itself. It is very common and has been found in this faunal assemblage in every known region except the southern Appalachian area.

Raaschella's closest relationship appears to be with the small genus *Acrocephalites*, which in the United States Upper Cambrian section occurs in the succeeding *Camaraspis* fauna.

RAASCHELLA ORNATA

Lochman, n. sp.

Plate 18, figures 6–10

Cranidium with a convex, broadly conical glabella with a straight anterior margin; two pairs of short deep glabellar furrows; dorsal furrow broad and deep at sides of glabella, but narrowing around the front. Fixed cheeks one-third width of glabella, very slightly convex; palpebral lobes small, narrow; palpebral furrow extremely narrow; frontal limb slightly wider than frontal border; transverse furrow faint, narrow, obsolete at median line. Posterolateral limbs long, marked by a broad shallow intramarginal furrow. Free cheek narrow, elongate, genal angle rounded. Facial suture cutting anterior margin near center of cranidium.

Pygidium transverse, triangular in outline; axial lobe convex, narrow, tapering posteriorly, divided into five segments and a terminal part; pleural lobes wide, flat, sloping abruptly down at outer margin, divided into four segments, the outer ends of which are raised and turned abruptly backward; pleural segments marked by faint narrow pleural furrows; narrow marginal border. Outer surface of test covered with minute granules; inner surface minutely punctate. Largest cranidium, 3×3 mm.; pygidium 4×2 mm.

There is a decided tendency in this species toward an obsolescence of the ridges and furrows on the outer surface of the test. This feature is especially noticeable in the larger specimens. On the cranidium the ocular ridge and transverse furrow are more sharply defined on the inner surface. On the adult pygidium only three pleural segments can be distinguished, whereas four are seen on the smaller pygidia.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Aphelaspis* zone). Holotype (a cranidium, U. S. Nat. Mus. 95524) and paratypes (a cranidium, a pygidium, and a free cheek, U. S. Nat. Mus. 95525) from outcrop along Mill

Creek road 2 miles south of Mason, Mason County, Tex.

DEIRACEPHALUS ASTER (Walcott)
Plate 18, figures 1, 2

Acrocephalites? aster, WALCOTT, *1916*, Smithsonian Misc. Coll., vol. 64, no. 3, p. 178.
Deiracephalus aster (Walcott), RESSER, *1935*, Smithsonian Misc. Coll., vol. 93, no. 5, p. 22.

Original description:

This is a very distinct species. The narrow median swelling on the frontal limb is much like that of *Acrocephalites stenometopus*, and unlike the boss on other species referred to the genus.

The occipital spine is broken off the specimen represented by figure 9b, but it is finely shown as a cast in the shale matrix, where it has been removed by solution.

This species is a relatively rare member of the *Cedaria* fauna. Only one partly complete cranidium has been obtained.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Figured cranidium (Mount Holyoke Mus. 654) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

METEORASPIS BIPUNCTATA
Lochman, n. sp.
Plate 17, figures 4–8

Cranidium narrow and elongate; glabella conical, strongly convex; no trace of glabellar furrows; occipital furrow narrow and deep; occipital ring of medium width, convex; dorsal furrow narrow and deep, outlining glabella. Fixed cheeks slightly convex, extremely narrow, only one-eighth the width of glabella; palpebral lobes medium sized, crescentiform, situated on transverse median line of glabella; palpebral furrow broad and shallow; no ocular ridge; frontal limb narrow, vertical; transverse furrow broad and deep, marked with two small shallow pits, one on each side of median line; frontal border of medium width, very convex; anterior margin rounded. Posterolateral limbs short and narrow, marked by a narrow deep intramarginal furrow. Facial suture cutting anterior margin near center of cranidium, curving out to transverse furrow and then running back to palpebral lobes around which it curves, thence passing diagonally outward and backward to cut posterior margin within genal angle. Pygidium not known.

This species is a very distinctive and well-represented member of the *Cedaria* fauna. It differs in several well-marked features—the greater elevation of the fixed cheeks and the shape and convexity of the glabella—from the other described species, *M. metra* (Walcott), of which the exact stratigraphic horizon is unknown.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Holotype (a cranidium, U. S. Nat. Mus. 95526) and paratype (a cranidium, U. S. Nat. Mus. 95527) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

Order PROPARIA Beecher
Family NORWOODIDAE Walcott

NORWOODIA TENERA Walcott
Plate 18, figures 11–13

Norwoodia tenera WALCOTT, *1916*, Smithsonian Misc. Coll., vol. 64, no. 3, p. 172.

Original description:

In general form the dorsal shield of this species resembles that of *N. simplex*, but in details it is quite distinct. It has eight thoracic segments, the pleural lobes of which have a very narrow pleural furrow and slightly falcate ends; a slender median spine occurs on the third, fifth, and seventh segments of the axial lobe . . . .

Surface minutely granular with a few larger scattered granules on the cephalon, thoracic segments, and pygidium.

The largest entire specimen has a length of 3.5 mm.

Cranidium.....1.5 mm.
Thorax.....1.5 mm.
Pygidium.....0.5 mm.

The largest cranidium in the collection has a length of 4 mm., which on the basis of the entire dorsal shield mentioned would give a total length of about 9.5 mm.

This small, neat species is abundant on

two or three thin layers of shaly limestone of the Weeks formation.

A number of well-preserved cranidia from the *Cedaria* fauna are referred to this species.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Figured cranidium (Mount Holyoke Mus. 657) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

Family MENOMONIDAE Walcott

MILLARDIA MAGNAGRANULATA
Lochman, n. sp.
Plate 18, figure 3

Cephalon transversely elongate, strongly convex, genal angles rounded; glabella subtriangular, convex; occipital ring of moderate width and convexity; occipital furrow deep and narrow; dorsal furrow narrow. Fixed cheeks narrow, highly elevated; palpebral lobes small, crescentiform, situated opposite the anterior end of glabella; frontal limb short, concave; frontal border narrow, convex. Posterolateral limbs elongate, narrowing to a point at genal angles, marked by a narrow intramarginal furrow. Free cheeks large, elongate, and convex, with small elevated eye at the inner angle. Facial suture indistinguishable in front of palpebral lobes; behind them passing diagonally outward and then curving abruptly downward and backward to cut the lateral margin anterior to the genal angle. Pygidium not known.

Outer surface of cheeks and limbs covered thickly with large and small granules; glabella sparsely covered with large granules.

One well-preserved cranidium and several fragments are referred to this species. *Millardia magnagranulata* is most closely related to *M. avitas*, from which it differs in the distinctive surface ornamentation and the course of the facial suture.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Holotype (a cranidium, U. S. Nat. Mus. 95015) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

MILLARDIA AVITAS Walcott
Plate 18, figures 4, 5

Millardia avitas WALCOTT, *1916*, Smithsonian Misc. Coll., vol. 64, no. 3, p. 165.

Original description:

This species is represented by two very distinct cranidia. These differ in so many respects from the other species of the genus that detailed description and comparisons do not appear to be necessary. The most nearly related form is *M. optata* from the Upper Cambrian of Wisconsin. With a strong lens the surface is seen to be roughened by minute granules of varying size.

One incomplete but well preserved cranidium and an unusual thoracic fragment of this species occur in the highest beds of the *Cedaria* zone. The fragment of the thorax is composed of the posterior third of the cranidium and the first six thoracic segments, nearly complete. The specimen is preserved in the same medium-grained crystalline limestone as the rest of the fauna.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Cedaria* zone). Figured cranidium (Mount Holyoke Mus. 655) and figured thoracic fragment (Mount Holyoke Mus. 656) from the southwest side of Lion Mountain on Highway 29 about 9 miles northwest of Burnet, Burnet County, Tex.

PHYLUM UNDETERMINED

PEMPHIGASPIS INEXPECTANS
Lochman, n. sp.
Plate 17, figures 27, 28

Shield subcircular in outline, distinctly trilobate; posterior margin straight near center and curving forward at sides; median lobe narrow, tapering rapidly towards the anterior end, regularly annulated; lateral lobes subelliptical, very convex, with sides incurved to the ventral surface. Outer surface of test roughened by fine irregular venations.

Only one slightly damaged specimen of this peculiar genus has yet been found in the Texas material, but its occurrence is of particular interest as here also it is a rare form in the *Crepicephalus* fauna. A third occurrence of the genus has recently been recorded from the central Appalachian area. *Pemphigaspis* cf. *P. bullata* Hall is reported by Dr. Charles Butts from the Warrior limestone of Pennsylvania (2).

Pemphigaspis inexpectans differs from *P. bullata* of Wisconsin in its nearly circular outline, which is caused by the more rapid anterior tapering of the medial lobe combined with the posterior narrowing of the lateral lobes. Unfortunately the Texas species does not add any information concerning the true relationship of this peculiar form.

Occurrence.—Upper Cambrian, Cap Mountain formation (*Crepicephalus* zone). Holotype (U. S. Nat. Mus. 95016) from outcrop in bed of South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

Phylum BRACHIOPODA

Order ATREMATA Beecher

Family OBOLIDAE King

LINGULELLA ARGUTA (Walcott)

Plate 18, figures 17–19

Lingulella arguta (Walcott), WALCOTT, *1912*, U. S. Geol. Survey Mon. 51, p. 478.
Lingulella acutangula (Roemer), WALCOTT, *1912*. U. S. Geol. Survey Mon. 51, p. 474.

Supplementary description:

General form elongate ovate, with ventral valve acuminate and dorsal valve ovate in outline; ventral valve averaging 10×10 mm. with greatest width anterior to median line; convexity 1 mm; dorsal valve averaging 9×8 mm.; convexity 1.5 mm. Shell composed of an outer thick layer and numerous thin inner lamellae set obliquely to outer layer. Outer surface marked by regular concentric lines of growth, both well defined and faint, and covered in the intervening area by a distinctive pattern of very short, irregular, imbricating ridges; inner lamellae showing concentric growth lines crossed by innumerable fine radiating striae; innermost lamellae covered with large punctae arranged in concentric rows.

Interior of ventral valve having a large elongate club-shaped visceral area, with apparently a narrow median septum; central muscle scars situated at the anterior lateral corners of visceral area.

Interior of dorsal valve with a narrow elongate visceral area marked by a faint median septum; medium-sized oval central muscle scars lying slightly anterior to transverse median line; smaller anterolateral muscle scars situated well forward in shell; course of main vascular sinuses and parietal band well defined.

This species of *Lingulella* is a very common member of the *Aphelaspis* fauna. For a discussion of the synonymy and identification of this form see the discussion under *L. acutangula* (Roemer) (3).

Occurrence.—Upper Cambrian, Cap Mountain formation (*Aphelaspis* zone). Hypotypes (U. S. Nat. Mus. 95017) from outcrop on road along South Fork of Morgan Creek 4.2 miles northwest of Highway 29, Burnet County, Tex.

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STUDIES OF LATE PALEOZOIC AMMONOIDS

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I. METHODS OF DRAWING SUTURES; BIBLIOGRAPHY

ABSTRACT

This paper, the first of a series, describes the technique of drawing the sutures of ammonoids and lists the publications on late Paleozoic ammonoids of Kansas and adjacent regions.

The main purpose of the series of papers of which this is the first is to record and describe some late Paleozoic ammonoids from Kansas and to compare them with contemporaneous forms from elsewhere. Although Paleozoic ammonoids are by no means common in Kansas, our knowledge of these important fossils has progressed rapidly during the past few years. The list of horizons and forms from the northern mid-continent region begins to look almost as impressive as the record of ammonoids from the contemporaneous beds of Texas—exclusive of the post-Wolfcamp and post-Wichita beds of Texas, which have no corresponding marine equivalents in Kansas and northern Oklahoma. Furthermore, the ammonoids from the northern midcontinent region furnish new additional forms previously unknown from Texas or elsewhere.

Late Paleozoic ammonoids have recently been collected in Kansas and adjacent parts of Missouri and Oklahoma by Messrs. Bridwell, Carpenter, Jewett, Kleihige, myself, and by other persons. Some of these ammonoids have been described, and descriptions of a few others are in preparation. Extensive and valuable contributions (partly unpublished) to the knowledge of the ammonoids of the northern mid-continent region have recently been made by A. K. Miller alone and in coöperation with J. B. Owen and L. M. Cline, and by F. B. Plummer and Gayle Scott. A complete list of publications is appended.

It is believed that ammonoids, fusulinids, some fenestrate bryozoans, and selected terrestrial plants are most important for correlation of the late Paleozoic rocks of Kansas and Texas and of the rest of the world. The remarkable development in the study of these fossils in the past decade has thrown new light on the problem of correlation of the late Paleozoic strata, but there is still great need for further improvement in our technique in the use of fossils in stratigraphy so that they may serve still better the great need of precise and detailed correlation. The harmonious development of detailed and precise morphologic and ontogenetic study of fossils (including, when necessary, biometric analysis), combined with the evaluation of their significance as time indicators apart from their significance as indicators of environments, and finally

a determined attempt to reconstruct their step-by-step evolution are considered essential for success in their use for future exact and detailed intra- and inter-continental correlations. It is in the spirit of this kind of research in stratigraphic paleontology that this series of articles is contemplated.

METHOD OF DRAWING SUTURES

Because the study of the suture is most important for the generic and specific distinction of ammonoids, it is essential that the outlines of sutures, as they appear on the inner molds of the shells, be traced on a plane surface with the greatest possible precision. Precision becomes particularly important in the cases where comparatively slight differences in the pattern of sutures, such as the degree of curvature and the angularity of apices, enter into specific and even generic characteristics of ammonoids. If the making of the illustrations is left to an artist without rigid control by a paleontologist, unwarranted generalizations are liable to blur the picture of the actual characters of the suture. When studying the literature on late Paleozoic Glyphioceratidae, whose complete external mature suture consists only of five simple saddles and four simple lobes, I found that a somewhat greater faithfulness in reproduction of these sutures than usually practiced is generally desirable. At the same time I found that the shape of the suture varies in every species and in every individual. It appears that occasionally this variability led to conscious or unconscious generalizations by paleontologists themselves, which is perhaps justified at a certain stage of our knowledge of ammonoids, but which I believe is not desirable when finer distinction of these stratigraphically important fossils is attempted. A student of ammonoids can usually illustrate only one typical suture for each species that he recognizes, and therefore he has the choice of selecting, more or less at random, a suture that he views as being most typical for the species, or of constructing a generalized outline as a sort of average suture design. The first procedure is certainly the better and is usually followed. However, in either case, the character and limits of variation of suture within an individual and a species is not considered, and usually the reader is left to discover these variations on photographs of specimens, many of which are not particularly adapted for this purpose.

In order to give a complete, precise, and impartial idea of the shape of the sutures of the ammonoids studied, I show as a rule more than one suture for each individual illustrated and for each stage of growth except the earliest, where only one suture for each stage is given. By doing so the spacing of the sutures is also shown—a feature that may be of specific importance, as the following description of *Goniolobo-ceras goniolobum* and *G. welleri* seems to indicate. The same general plan of illustration of variations of suture within a species was followed in my earlier paper on *Baculites*, *Scaphites*

and other late Cretaceous ammonoids of western Kansas (4, pp. 289–363). In such complicated sutures as those of *Baculites* or of *Perrinites* of the late Paleozoic, still greater attention must be given to changes in the suture with change of diameter of the conch. Precise indication of the diameter or radius at which the particular suture has been taken is desirable for the sake of detailed comparison with similar forms observed at somewhat different horizons.

All these remarks are given chiefly as a memorandum for the technical part of the study of ammonoids, as undoubtedly most modern students of these fossils are aware of the importance of the distinctive features outlined. The drafting of sutures onto a plane requires careful and skillful technique, and various methods are followed by different students. I use the method outlined in my paper of 1933:

> In preparing the sketches of the sutures of *Baculites* and other Ammonoidea of the Pierre two methods were used. The larger sutures were traced directly on cellophane, which was wrapped around a portion of a fossil. In order to add visibility and avoid mistakes in tracing, the space between two neighboring sutures was painted with black India ink. A fine drafting pen was used for painting the minute dentations of the sutures. Cellophane is preferable to other transparent material (celluloid film, wax paper, tracing cloth, etc.) because it is perfectly transparent, and, being soft and flexible, can be pressed more tightly against the uneven surface of the variously sculptured molds of ammonoids. The India ink sticks to cellophane fairly well, and fine lines can be drawn on it. However, when drawing a line over those places where the cellophane is not quite firmly pressed against the surface of the fossil, one inevitably scratches the soft tissue with the sharp point of the pen. Owing to this the lines soon become too heavy to express the finer details of the sutures. The writer found that it is much safer and more convenient not to trace on cellophane the suture lines themselves, but to ink in the space on one side of a suture.
>
> The next operation is the final tracing from the cellophane drawing. Due to slight warping of the cellophane painted with India ink, the use of a light-table (table with glass top illuminated from below) is recommended. If desirable the cellophane copy can be enlarged by photography and the final tracing of the suture can be made from the photograph. In view of the desirability of having the drawings two times larger than the proposed size of printed illustrations the enlargement by photography is ordinarily preferable.
>
> For the tracing of very small and complicated sutures the method of direct tracing on cellophane is too crude. For drafting of the sutures of juvenile stages of *Baculites* and, also, of the sutures of smaller coiled scaphites, the writer used a camera-lucida attached to a microscope. In order to draw an undistorted suture on a plane, several settings of the specimen must be made. For a curved surface of about 180 degrees, or half way around a shell, the writer made six or seven settings. After a part of a suture is copied, the fossil is turned so as to have the next portion of the suture nearly perpendicular to the axis of the microscope. In order not to depart from a constant orientation of the shell one must revolve it around the same or nearly the same axis, and in order to make proper connection of two neighboring portions of a suture the comparatively undistorted edges of the drawings of the two must somewhat overlap each other. The smallest magnification of ordinary microscopes used in paleontological laboratories with attached camera-lucida is about 10 times and, therefore, the drawn suture is usually too large and must be reduced. This can be done by photography or by a pantograph (4, pp. 290, 293).

The sutures of the described late Paleozoic ammonoids, when taken

directly from the specimens by the method of tracing on wrapped cellophane, have been enlarged photographically two times and reduced back to natural size in reproduction for publication.

The following is a reasonably complete annotated bibliography of the Late Paleozoic ammonoids from Kansas and Missouri.

REFERENCES AND ANNOTATED BIBLIOGRAPHY

1. BEEDE, J. W., and ROGERS, A. F., *1908*, Faunal divisions of the Kansas Coal Measures: *Kansas Univ. Geol. Survey*, vol. 9, pp. 318–385.

   Species of Pennsylvanian ammonoids are listed on pl. XLII (facing p. 328) and in "Systematic chart," pp. 371 and 383. The species have not been described; they were not found by me in the University of Kansas collection. The same ammonoids were previously listed by the same authors in a series of "Coal Measure Faunal Studies" published in *Kansas Univ. Quart.*, vol. 9, 1900, pp. 233–254, *Kansas Univ. Sci. Bull.*, vol. 1, pp. 163–181, and *Ibid.*, vol. 2, pp. 459–473.

2. BISAT, W. S., *1931*, On the occurrence of a British coal measure goniatite in Missouri, U. S. A.: *Yorkshire Geol. Soc. Proc.*, vol. 22, pp. 1–8, 5 text figures, 1 plate.

   Describes and illustrates *Homoceratoides jacksoni* Bisat and *Gastrioceras welleri* Smith from the upper Des Moines near Clinton, compares them with ammonoids of Great Britain, and suggests a tentative correlation of the strata of America and Great Britain.

3. BROADHEAD, G. C., *1873*, Geology of northwestern Missouri: *Missouri Geol. Survey Prelim. Rept.*, Iron ores and coal fields, pp. 1–213.

   Ammonoids from several localities in Missouri are listed on pp. 61, 111, 198–199, 393–394. Localities, stratigraphic horizons, and good geologic sections, which yielded the ammonoids, are given and are helpful in subsequent search for ammonoids.

4. ELIAS, M. K., *1933*, Cephalopods of the Pierre formation of Wallace County, Kansas: *Kansas Univ. Sci. Bull.*, vol. 21, pp. 289–363.

5. ———, *1936*, Late Paleozoic plants of the midcontinent region as indicators of time and of environments: *16th Internat. Geol. Cong. Rept., U. S. A., 1933*, vol. 1, pp. 691–700.

   Gives (pp. 693, 694) a brief critical review of previous publications on ammonoids from Kansas and Missouri and charts (p. 694) the stratigraphic position of known ammonoids, including those identified by the author.

6. GIRTY, G. H., *1903*, Tabulated list of invertebrate fossils from the Carboniferous section of Kansas, in ADAMS, G. I., GIRTY, G. H., and WHITE, DAVID, Stratigraphy and paleontology of the upper Carboniferous rocks of the Kansas section: *U. S. Geol. Survey Bull.* 211, pp. 73–83.

   Ammonoids from a few localities in Kansas are recorded (p. 83). Through the kindness of Dr. Girty I have seen the specimens in the collection of the U. S. Geological Survey. All seem to be immature forms and are valuable chiefly as indicators of horizons and localities of the ammonoids in Kansas, from which possibly some additional material may be secured.

7. ———, *1915*, Invertebrate paleontology, in HINDS, H., and GREENE, F. C., The stratigraphy of the Pennsylvanian series in Missouri: *Missouri Bur. Geology and Mines*, vol. 13, 2d ser., pp. 263–375, pl. 27–32.

   Goniloboceras parishi (Miller and Gurley) and *Gastrioceras welleri* (Smith) are briefly described (p. 369) but not illustrated. Exact localities and horizons are given (pp. 364–374).

8. KEYES, C. R., *1894*, Paleontology of Missouri, Part 2: *Missouri Geol. Survey*, vol. 5, pp. 1–266, pls. 33–55.

   A single goniatite from the upper coal measures of Kansas City, Mo., is illustrated (pl. 56, fig. 1).

9. MEEK, F. B., and WORTHEN, A. H., *1866*, Description of invertebrates from the Carboniferous system: *Illinois Geol. Survey*, vol. 2, Paleontology, pp. 143–470, 39 text figs., 32 pls.

   Goniatites globulosus Meek and Worthen from Kansas is described and illustrated (pp. 390–392). Subsequently it was made the type of *G. globulosus* var. *excelsus* (see Meek, 1876).

10. MEEK, F. B., *1876*, Notice of a very large goniatite from eastern Kansas: *U. S. Geol. Survey Terr. Bull.* 1, No. 6 (2), p. 445.

    The very large smooth ammonoids from Kansas previously classified as *Goniatites globulosus* are designated as *G. globulosus* var. *excelsus* Meek.

11. MILLER, A. K., *1936*, A species of the ammonoid genus *Artinskia* from the Lower Permian of Kansas: *Jour. Paleontology*, vol. 10, pp. 490–496, 6 text figs. and 1 pl.

A new species, *Artinskia worthani*, is described and illustrated in detail and its relation to previously known medlicottids is analyzed.

12. MILLER, S. A., and FABER, C., *1892*, Descriptions of some sub-Carboniferous and Carboniferous Cephalopoda: *Cincinnati Soc. Nat. History Jour.*, vol. 14.

Goniatites missouriensis Miller and Faber from the Missouri group at Kansas City, Mo., is illustrated and described. It is now classified as *Schistoceras*.

13. MILLER, S. A., and GURLEY, W. F. E., *1896*, New species of Paleozoic invertebrates from Illinois and other states: *Illinois State Mus. Nat. History Bull.* 11.

Describes and illustrates *Goniatites parrishi* Miller and Gurley (=*Goniolobоceras*) and *G. kansasensis* Miller and Gurley (=*Gastrioceras*) from the group at Kansas City, Mo.,

14. NEWELL, N. D., *1936*, Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda: *Jour. Paleontology*, vol. 10, pp. 481–489, 2 text figs. pls. 68–72.

Pronorites kansasensis Newell from the Argentine limestone, Missouri group, at Kansas City, Kans., is described and illustrated.

15. PLUMMER, F. B., and SCOTT, GAYLE, *1937*, Mississippian, Pennsylvanian and Permian ammonoids of Texas: *Geology of Texas*, vol. 3, pt. I, 350 pp., 77 text figs., 41 pls.

Gives a new list of identified species from the locality at Emporia, Kans. The collection was previously identified by Wiedey and Smith (see Smith, J. P. 1929).

16. SAYRE, A. N., *1930*, The fauna of the Drum limestone of Kansas and western Missouri: *Kansas Univ. Sci. Bull.*, vol. 19, pp. 75–263, 1 text fig., 21 pls.

Goniolobоceras parrishi (Miller and Gurley)? *Goniolobоceras goniolobum* (Meek), and *Schistoceras missouriensis* (Miller and Faber) are described and illustrated (pp. 156–158, pls. 18 and 21). The photographs are about ¾ natural size. The originals are in the University of Kansas paleontological collection.

17. SHUMARD, B. F., *1855*, Paleontology: *Missouri Geol. Survey*, vol. 2.

Goniatites planorbiformis Shumard (=*Gastrioceras*) from the upper coal measures at Kansas City, Mo., is illustrated and described.

18. ———, and SWALLOW, G. C., *1858*, Description of new fossils from the Coal Measures of Missouri and Kansas: *Acad. Sci. St. Louis Trans.*, vol. 1, pp. 198–227.

Describes but does not illustrate *Goniatites minimus* Shumard from the "Middle Coal Measures," Missouri, *Goniatites? parvus* Shumard from the "Upper Coal Measures," Kansas, and *Goniatites? politus* Shumard from the "Middle Coal Measures," Missouri.

19. SMITH, J. P., *1903*, Carboniferous ammonoids of America: *U. S. Geol. Survey Mon.* 42, pp. 1–211, 29 pls.

Lists on pp. 15–16 the following ammonoids from Missouri and Kansas: *Milleroceras parrishi* Miller and Gurley, *Gastrioceras excelsum* Meek, *G. kansasense* Miller and Gurley, *G. planorbiforme* Shumard, *G. welleri* Smith,[1] *Schistoceras missouriense* Miller and Faber, and "*Goniatites*" *parvus* Shumard. They are described and illustrated on pp. 88–89, 91–92, 97, 98, 111, 127–128, 142, and on plates 8, fig. 1; 16, figs. 6–8; 17, figs. 9–11; 24, figs. 13–20; 28 and 29.

This monograph on the ammonoids of the two States is most valuable and is complete for its time. Some of the illustrations are somewhat generalized; when detailed comparison of new material is attempted, examination of the described types is necessary.

20. ———, *1929*, Transitional Permian ammonoid fauna of Texas: *Am. Jour. Sci.* 5th ser., vol. 17, pp. 63–80.

Ammonoids from Emporia, Kans., are listed (p. 67). The species have since been re-identified (see Plummer and Scott, 1937; see also note on p. 695 in Elias, 1936).

[1] In the original text *Gastrioceras subcavum* is listed among the forms from Missouri, whereas *G. welleri* is not. This error is here corrected in conformance with the text, where these two forms are described and correctly referred geographically.

NOTE: The manuscript of this paper was received by the editor March 1, 1937.

II. REVISION OF *GONIOLOBOCERAS* FROM LATE PALEOZOIC ROCKS OF THE MIDCONTINENT REGION

ABSTRACT

Gonioloboceras welleri has no ventral groove, as is erroneously indicated on its cross section by J. P. Smith. Furthermore its ventral saddle is notched in the same way as *G. goniolobum* and *G. gracile*. The genus *Gurleyoceras* Miller, which has been erected for the group of *Gonioloboceras* with grooved venter as erroneously supposed to exist in *G. welleri*, becomes a synonym of *Gonioloboceras*. *Milleroceras* Hyatt is also a synonym of *Gonioloboceras*. *Milleroceras parrishi* (Miller and Gurley), *M. minusculum* Miller, *Gurleyoceras discoidale* (Böse) Miller, and *Gonioloboceras gracellenae* Miller are the young of *Gonioloboceras goniolobum* or of *G. welleri*. The described early stages of these two species are very much alike, and only mature stages seem to be different. *Gonioloboceras welleri* may be the female of *G. goniolobum*, but it is more likely that they are specifically distinct, as the latter seems to be a somewhat earlier form, being found in the Missouri series of Kansas and Missouri, whereas *G. welleri* is known from the Wayland shale, Cisco group, of Texas, which is stratigraphically higher than the Missouri.

In the course of studies of the Pennsylvanian ammonoids from Texas, Oklahoma, and Kansas I noticed a discrepancy between the current conception of the conch of *Gonioloboceras welleri* and its actual character. In order to clear up the discrepancy I borrowed the types of this species from Stanford University through the kindness of Professor Siemon Müller. I am also indebted to Dr. George Girty, of the U. S. Geol. Survey, and to Dr. R. C. Moore, of the University of Kansas, for cordial permission to examine the ammonoids from Texas and Kansas in their respective collections.

METHOD OF STUDY

In the study of *Gonioloboceras* as well as other ammonoids, examination of the early stages of development is indispensable. The knowledge of the young is important not only for the establishment of the phylogeny of a form under consideration but also because some immature individuals are found alone. Unless we know exactly how the young of *Gonioloboceras goniolobum* and other *Gonioloboceras* is constituted, we may easily misidentify them and treat them as different species or even different genera. This is what actually happened in the case of *Gonioloboceras goniolobum* and *G. welleri*, the young of which, I conclude, have been described under the names *Milleroceras parrishi*, *Gonioloboceras gracellenae*, and *Gurleyoceras discoidale*. All these supposed species were established on specimens that are smaller than the mature form of either *G. goniolobum* or *G. welleri* and can be matched by young of these two species. The fact is that the earlier stages of *G. goniolobum* have not previously been demonstrated at all, and only the glyphioceran stage of *G. welleri* has been illustrated by Smith (13, p. 20, figs. 9–11). The next older stage, which I propose to call the milleroceran stage, remained undescribed. I studied the early stages of *G. goniolobum* by breaking a specimen collected by me from the oolitic Raytown limestone northwest of Kansas City, Kans. I traced the

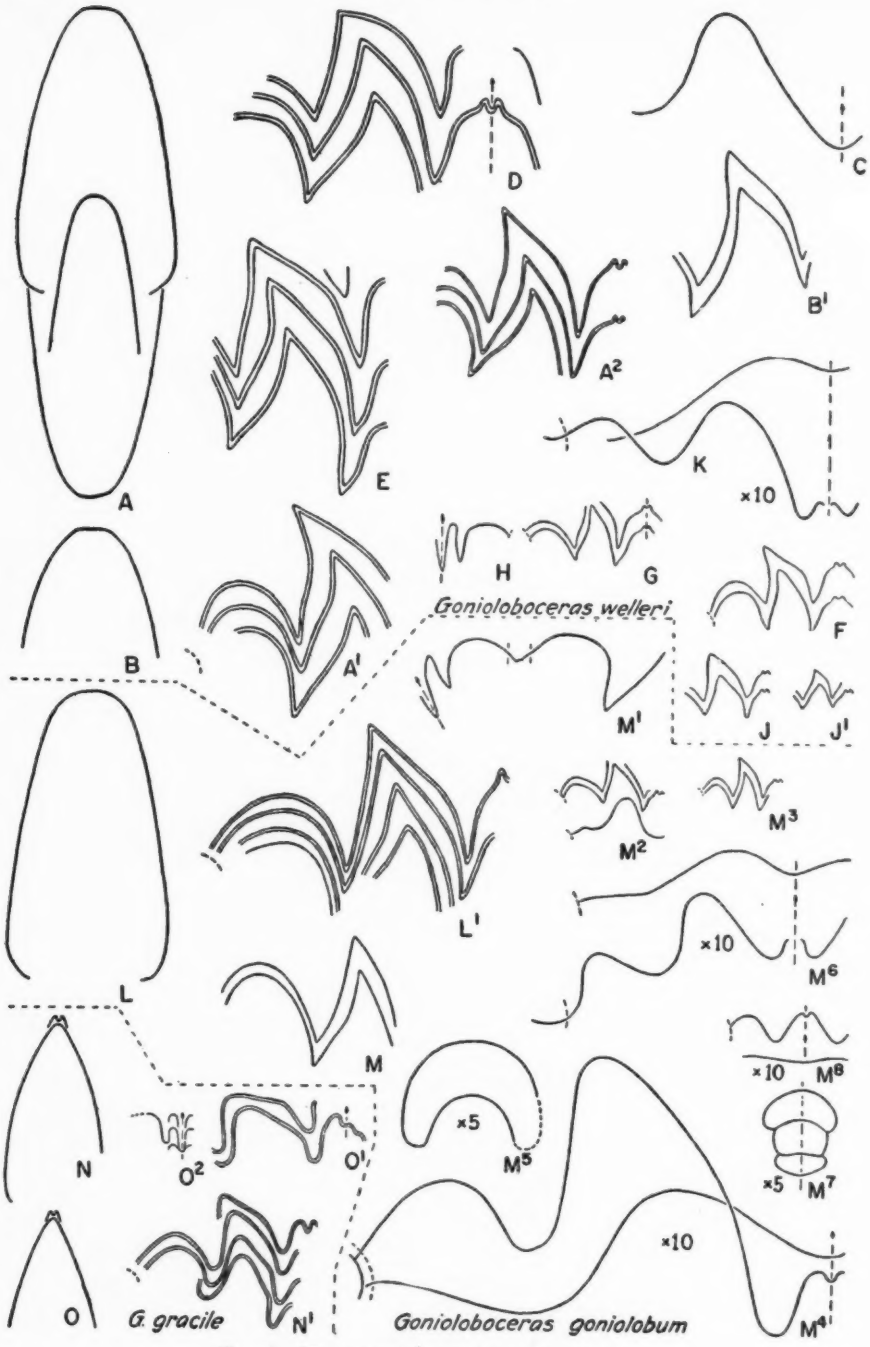

FIG. 1—*(See opposite page for explanation)*

corresponding early stages of *G. welleri* chiefly on mature paratypes from the Wayland shale, Texas, from which paratypes had been broken by J. P. Smith in order to expose the early sutures.

Genus GONIOLOBOCERAS
Hyatt, 1900

Goniolobоceras, HYATT, *1900*, Zittel's Textbook of paleontology (American edition), p. 551.—SMITH, *1903*, U. S. Geol. Survey Mon. 42, p. 123.—GIRTY, *1915*, U. S. Geol. Survey Bull. 544, p. 261.—MILLER, and CLINE, *1934*, Cephalopod fauna of the Pennsylvanian Nellie Bly formation of Oklahoma, Jour. Paleontology, vol. 8, p. 175.

Milleroceras, HYATT, *1900*, Idem, p. 550.—SMITH, *1903*, Idem, p. 127.—MILLER, *1932*, Jour. Paleontology, vol. 6, p. 69.

Gurleyoceras, MILLER, *1932*, Idem, p. 76.

Genotype: *Goniatites goniolobum* MEEK, *1877*

The genus *Goniolobоceras* was erected by Hyatt (3, p. 551) on *Goniatites goniolobus* Meek, and is characterized by "the flattened sides, narrow abdomen, and extremely angular lobes." The genotype came from an unknown horizon and locality, probably from the late Pennsylvanian of New Mexico, and is now lost. Illustrations and description indicate, however, that it had a rounded grooveless venter.

Another species of the genus, *Goniolobоceras welleri*, was described by J. P. Smith in his comprehensive monograph of the Carboniferous ammonoids of America. According to Smith the conch of this species is

smooth, compressed, with flattened sides and

EXPLANATION OF FIG. 1.

A to *K*—*Goniolobоceras welleri* Smith. *A*, A^1, A^2, Front view and sutures at radius of 39 mm. (diam. 62 mm.) and radius of 29 mm. (see lateral view on pl. 19, fig. 6), Kansas Univ. coll. 55M1-1; *B*, B^1, cross section and sutures at radius of about 38 mm. (see lateral view on pl. 19 fig. 7), Kansas Univ. coll. 55M2-1; *C*, line of growth at radius of about 41 mm. (see lateral and front views on pl. 20, figs. *6a*, *b*), Kansas Univ. coll. 55M-2; *D*, sutures at radius of 40 mm., holotype (see lateral and front views on pl. 19, figs. *1a*, *b*), Stanford Univ. coll. 5898; *E*, sutures at radius of about 41 mm. (see lateral and front views on pl. 19, figs. 5*a*, *b*), Kansas Univ. coll. 55M1–3; *F*, sutures at radius of 19 mm. (diam. 31 mm.), paratype (see front, side, and rear views on pl. 19, figs. 3*a*, *b*, *c*), Stanford Univ. coll. 5616; *G*, sutures at radius of 15 mm. (diam. 24 mm.) (see front, side, and rear views on pl. 19, figs. 8*a*, *b*, *c*), Kansas Univ. coll. 3472-1, type 231.1; *H*, internal suture at outer radius of about 23 mm. (diam. 37 mm.), Kansas Univ. coll. 55M2-2; *J*, J^1, sutures at radius of 13 mm. (diam. 22 mm.) and radius of 10 mm., paratype, Stanford Univ. coll. 5619; *K*, suture and shape of construction at radius of 4 mm. (diam. 7 mm.), paratype (see side and back views on pl. 19, figs. 4*a*, *b*), Stanford Univ. coll. 5618. All from Wayland shale, Graham formation, Cisco group, Texas; specimens 55M1 (coll. R. C. Moore) from locality 1 mile west of Graham and 55M2 (coll. R. C. Moore) from locality 4 miles northeast of New Castle, all natural size except fig. 14, which is ×10.

L to M^8—*Goniolobоceras goniolobum* (Meek). *L*, L^1, Cross section and sutures at radius of 41 mm. (see lateral view on pl. 20, fig. 4), oolitic Drum limestone, Kansas City, Mo. (coll. A. N. Sayre), Kansas Univ. coll. 357, type 123; *M* to M^8, external sutures—*M*, at radius of about 26 mm.; M^1, suture at radius of 22 mm., including internal suture; M^2, sutures and growth line at radius of 13 mm.; M^3, sutures at 10.5 mm. radius; M^4, suture and growth line at radius of 6.5 mm.; M^5, cross section, and M^6, suture and growth line at radius of 3 to 3.5 mm.; M^7, front view, and M^8, suture and growth line at radius of 1.3 mm. (see external side view and views of internal volution at diam. of 18 mm. on pl. 20, figs. 2*a*, *b*, *c* and 3*a*, *b* (from oolitic Raytown (?) limestone, Kansas City group, Missouri series, north of Boyn's quarry, Welborn, Wyandott County, Kans.) Kansas Univ. coll. 3473, type 232.1 (Coll. M. K. Elias). All natural size except figs. M^5 and M^7, which are ×5, and figs. M^4, M^6, and M^8, which are ×10.

N to O^2—*Gonioglyphioceras gracile* Girty. *N*, N^1, Cross section and sutures at radius of 23 mm.; *O*, O^1, O^2, cross section, external and internal sutures at radius of about 35 mm.; Boggy shale, sec. 35, T. 3 S., R. 7 E., Johnston County, Oklahoma, Kansas Univ. coll. 155 (coll. R. C. Moore).

narrow rounded venter at early maturity; angular and slightly furrowed at a later stage.

In the illustration of the cross section of the conch a very distinct furrow was shown (12, pl. 21, fig. 4), although there is no actual furrow, in the conch of *G. welleri*.

Unfortunately the erroneous conception introduced by Smith about the supposedly grooved venter of *G. welleri* misled A. K. Miller to select the species as the genotype of *Gurleyoceras*, a genus erected to receive the group of species of *Goniolobоceras* with furrowed venter (6, p. 76). In view of the fact that *Goniolobоceras welleri* actually has no ventral furrow, the genus *Gurleyoceras* becomes a synonym of *Goniolobоceras*. Dr. A. K. Miller, to whom I communicated the result of the study and demonstrated the types, expressed his agreement with this conclusion.

My subsequent studies of a large number of *Goniolobоceras* collected from various horizons in Texas, Kansas, and Oklahoma made me increasingly aware of the fact that *G. welleri* and *G. goniolobum* are so closely related that even their specific separation may be questioned. They are described here, however, as two different species, although their differences, if admitted, seem to be not quite of the same nature as originally supposed by J. P. Smith.

GONIOLOBOCERAS WELLERI Smith

Text figures 1, A to J[1]; plate 19; plate 20, figures 6a, b

Goniolobоceras welleri SMITH, *1903*, Carboniferous ammonoids of America: U. S. Geol. Survey Mon. 42, pp. 125–126, pl. 20, figs. 9–11 (young individuals), pl. 20, figs. 1–6 (fig. 4 is a drawing representing apparently a schematized section of fig. 3, but with erroneously shown ventral furrow).—PLUMMER and MOORE, *1912*, Stratigraphy of the Pennsylvanian formations of north-central Texas, Texas Univ. Bull. 2132, pl. 25, fig. 7 (opp. p. 189).—SMITH, *1932*, Lower Triassic ammonoids of America, U. S. Geol. Survey Prof. Paper 167 p. 24, pl. 43, figs. 1–3, refigured from earlier monograph (13), fig. 2 erroneously showing ventral furrow.

Gurleyoceras welleri MILLER, *1932*, Pennsylvanian cephalopod fauna from south-central New Mexico: Jour. Paleontology, vol. 6, p. 76.

Types: at Stanford University: 5898—Holotype, illustrated in U. S. Geol. Survey Mon. 42, pl. 21, figs. 3, 4(?), and 5, and in U. S. Geol. Survey Prof. Paper 167,

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EXPLANATION OF PLATE 19

Goniolobоceras welleri SMITH.

FIGS. 1*a*, *b*—Side and front views of holotype, natural size, Stanford Univ. coll. 5898 (13, pl. 21, fig. 3, in about ×⅔). (See sutures on fig. *D*.)

2*a*, *b*—Side and back views of paratype, Stanford Univ. coll. 5619; ×2.2. (See sutures on figs. *J*, *J*[1].)

3*a*, *b*, *c*—Front, side, and back views of paratype, Stanford Univ. coll. 5616 (13, pl. 21, figs. 1 and 2; very good-natural size reproductions from photographs). (See sutures on fig. *F*.)

4*a*, *b*—Side and back views of paratype, ×2.2, Stanford Univ. coll. 5618 (13, pl. 20, figs. 9–11, good photograph ×4 and front-view sketch; suture, fig. 11, generalized). (See suture and shape of constriction on fig. *K*.)

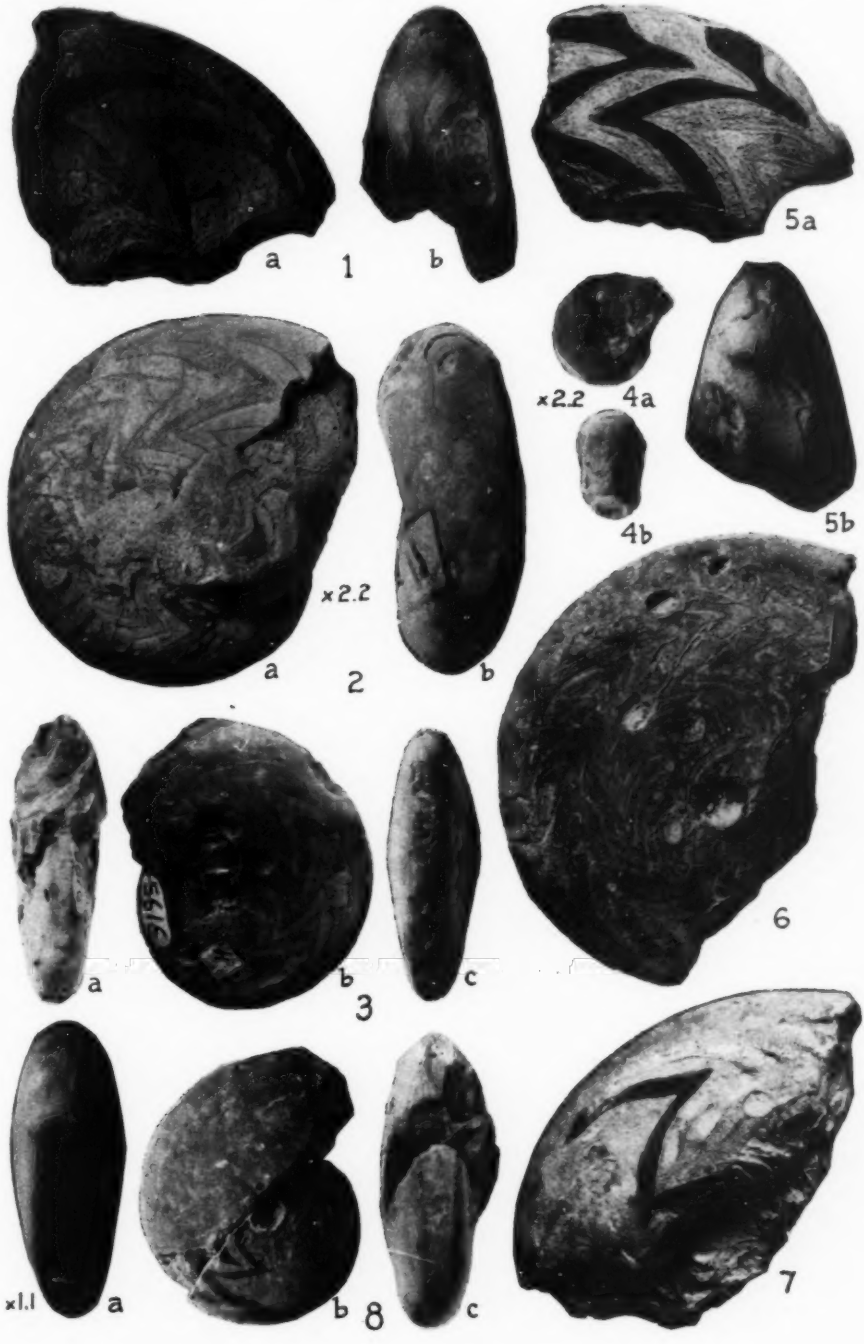
5*a*, *b*—Side and front views, Kansas Univ. coll. 55M1–3 (coll. R. C. Moore). (See suture on fig. *E*.)

6—Side view, Kansas Univ. coll. 55M1-1 (coll. R. C. Moore). (See front view and sutures on figs. *A*, *A*[1], and *A*[2].

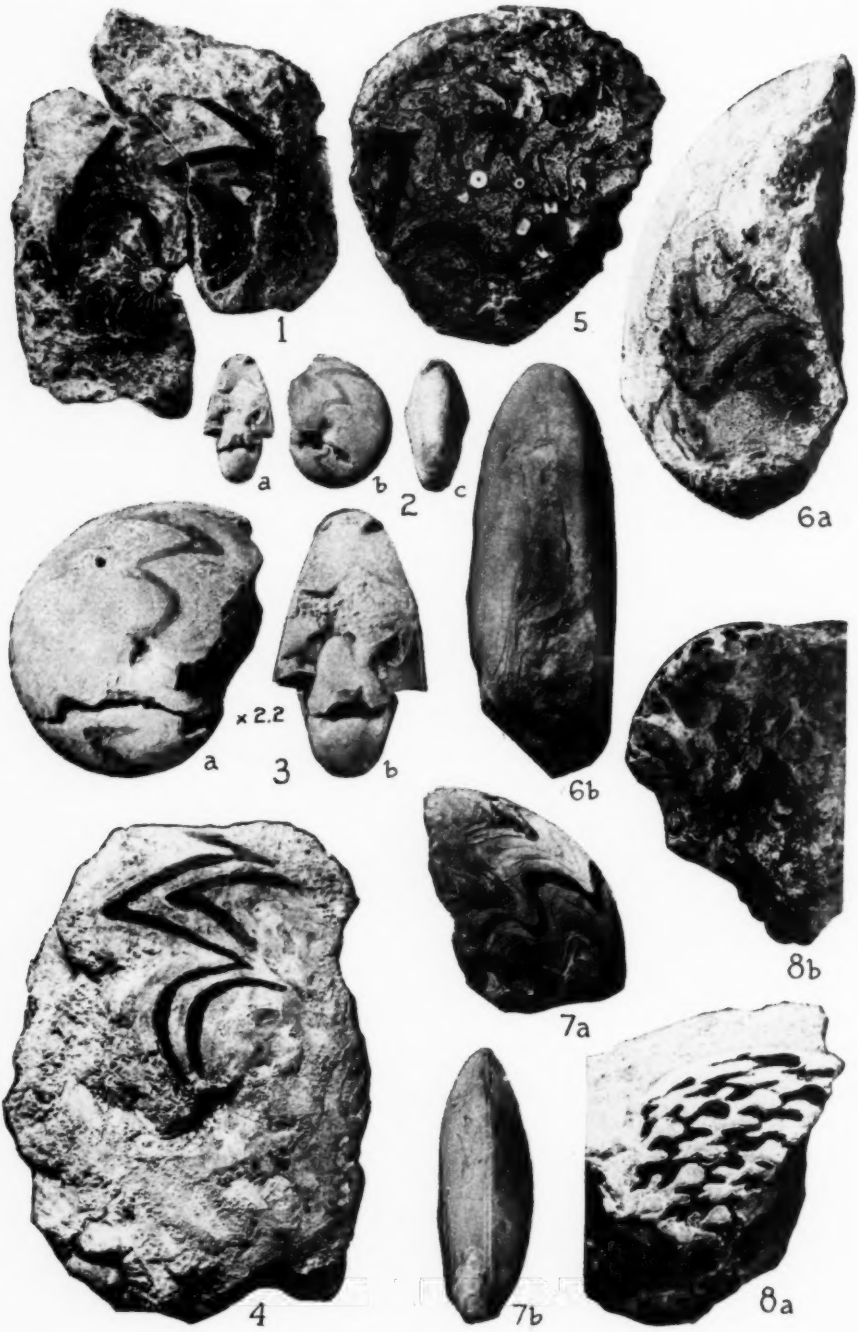
7—Side view, Kansas Univ. coll. 55M2-1 (coll. R. C. Moore). (See cross section and sutures on figs. *B*, *B*[1].) (This specimen has sutures somewhat like those in *G. goniolobum*, but it has cross section typical of *G. welleri*.).

8*a*, *b*, *c*—Back, side, and front views (*8a* ×1.1), Kansas Univ. coll. 3472–1, type 231.1 (coll. M. K. Elias). (See sutures on fig. *G*.)

All specimens from Wayland shale, Graham formation, Cisco group, Texas, except that shown in figs. *8a*, *b*, *c*, which is from Cedar Vale shale above Elmo coal, Wabaunsee group, 2 miles west and 3 miles south of Burlington Junction, Nodaway County, Mo. All natural size except as indicated.



Elias, Paleozoic Ammonoids



Elias, Paleozoic Ammonoids

pl. 43, figs. 2 (?) and 3. 5616—Paratype, Mon. 42, pl. 21, figs. 1 and 2, and Prof. Paper 167, pl. 43, fig. 1. 5618—Paratype, Mon. 42, pl. 20, figs. 9, 10, and 11. 5617, 5619, 5620—Paratypes, not illustrated by J. P. Smith. All collected by A. B. Grant from a locality west of Marr's Hall, Young County, Texas, Cisco group, Graham formation, Pennsylvanian.

Conch subdiscoidal or platycone, compressed, deeply involute with narrow umbilicus. Venter rounded, slightly flattened, but not grooved. Surface of conch smooth, with faint lines of growth. At the venter the lines swing back considerably, making a hyponomic sinus; they project forward prominently in the ventrolateral part of the conch, producing linguae, and make another but very gentle forward swing not far from umbilicus. Siphuncle has extreme marginal position directly below the ventral portion of conch. Collapse of shell wall above siphuncle occasionally produces an extremely gentle and regular to coarse and quite irregular depression in the middle of the venter, which might have lead J. P. Smith to the erroneous conception of the supposedly grooved venter in *G. welleri*.

External suture consisting of two pairs of very sharp lateral lobes and one sharp umbilical lobe. Ventral saddle only half as high as the first lateral, and provided with a small tongue-shaped and notched extension. First lateral saddle the most prominent, with convex ventral and concave dorsal sides. Second lateral saddle broadly rounded. Internal suture consisting of three narrow and sharp lobes, the middle or dorsal lobe being the longest. The two dorsal saddles are narrow and are rounded at the apex; the two lateral saddles are wide and broadly rounded.

The glyphioceran stage of *G. welleri* was illustrated by Smith from paratype 5618 of this collection (13, pl. 20, figs. 9–11). Because the suture for this specimen, as illustrated on his pl. 20, fig. 11, is obviously generalized (compare for instance with the sutures as correctly shown in the side view, pl. 20, fig. 9), I have prepared a new camera-lucida drawing of the suture from this paratype (fig. K, text fig. 1). Note that the first lateral saddle is not broadly rounded as illustrated by the artist in Smith's monograph but is somewhat subangular; the first lateral lobe is, on the contrary, gently rounded and not subangular. The second lateral lobe is on the umbilical wall, in mature *G. welleri*. This lobe is not sharp, as shown on Smith's drawing but is very gently rounded. The largest diameter of this individual is 7 mm. and the

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EXPLANATION OF PLATE 20

FIGS. *6a, b—Goniloboceras welleri* Smith, side and back views of fragment of living chamber with very distinct lines of growth, Kansas Univ. coll. 55M1-2 (coll. R. C. Moore). (See line of growth on fig. *C*, from Wayland shale, Graham formation, Cisco group, 1 mile west of Graham, Tex. Four of the visible lines of growth of the specimen are emphasized by pencil marks.)

1, 2a, b, c; 3a, b—Goniloboceras goniolobum (Meek), side view of external volution (fig. *1*), and front, side, and back views of internal coils obtained by breaking the specimen. Kansas Univ. coll. 3473, type 232.1 (coll. M. K. Elias). (See sutures, growth lines, and cross sections on figs. *M-M*^{7}, from oolitic Raytown (?) limestone, Kansas City group, Missouri series, west of Boyn's quarry, Welborn, Wyandotte County, Kans.

4—Side view, Kansas Univ. coll. 357, type 123 (coll. A. N. Sayre) (see cross section and sutures on figs. *L*, *L*^{1}), (12, pl. 21, fig. 5, $\times\frac{3}{4}$), from oolitic Drum limestone, Kansas City group, Missouri series, at Kansas City, Mo.

7a, b—Gonioglyphioceras gracile (Girty), side and back views, Kansas Univ. coll. 155-1 (coll. R. C. Moore) (see cross section and sutures on figs. *N*, *N*^{1}), from Boggy shale, sec. 18, T. 3 S., R. 7 E., Johnston County, Oklahoma.

8a, b—Properrinites plummeri Elias n. gen., n. sp., side and front view of holotype, Kansas Univ. coll. 890 (coll. J. H. Bennett), from Neva limestone, Big Blue series, east of Beaumont, Kans. All natural size except figs. *3a, b*, which are $\times 2.2$.

suture has been taken near the end of its outer volution. The conch is 4.5 mm. wide, or only 1½ times as wide as thick (ellipsocone of Bisat). Two constrictions per volution are observed. They are slightly curved, as shown in fig. K, text fig. 1.

The next stage of development, milleroceran, can be observed on paratype 5619 of Smith's collection (see figs. J, J[1]), which was not illustrated by him. This individual is 24 mm. in diameter and about 9 mm. thick. (Measurements are not very accurate because one side of specimen is broken at umbilicus.) The milleroceran stage of the suture, which is characterized by being widely acuminate and rounded at the tip, instead of having a sharply acuminate apex of the first lateral saddle, can be observed in this individual only on volutions not larger than 9 mm. in radius; but on the outermost three-quarters of a volution the goniolobocerас stage of suture, with sharply acuminate first lateral saddle, is developed.

When describing *Goniolobocerас welleri*, Smith differentiated it from *G. goniolobum* because it has

> the sides somewhat more flattened, is more compressed laterally, and at maturity has the venter narrow, angular, and slightly furrowed; also the ventral saddle is not notched, but has a tongue-shaped forward extension.

Smith adds that these differences "may be due to individual variation or to incorrect drawing of Meek's type" (12, p. 125). The latter statement makes clear that he made his comparison not with the type of *G. goniolobum*, but with its illustration by Meek. Probably the type of *G. goniolobum* which is now lost, was then already lost. The comparison between the two species, as revised here, is based not only on the figures of *G. goniolobum* by Meek but also on actual specimens identified by Sayre and me from Kansas and Missouri (see description of *G. goniolobum*, p. 98). My revised comparison has been made with fairly open mind in regard to the possible specific identity or nonidentity of *G. welleri* and *G. goniolobum*.

The difference in shape was found to be slight and not easily expressed in exact figures of form ratio or even in qualitative descriptive terms. Perhaps it is best to state that the venter of *G. goniolobum* is broader than that of *G. welleri*, which is not only narrower but distinctly flattened. However, in view of the fact that venters are more or less broad and rounded in both species, this difference between the two cannot be easily observed except on mature individuals.

The absence of a ventral furrow in *G. welleri* has already been pointed out; there is no distinction in this respect between the two species.

The construction of the ventral saddle in these species is also quite the same, contrary to the opinion of Smith. The apex of the ventral saddle in both *G. goniolobum* and *G. welleri* is provided with a tonguelike extension, which is notched in both forms. The notch is occasionally obscured through poor preservation or erosion, but it can be observed on all well-preserved venters of *G. welleri* from the Wayland shale and elsewhere; it is well developed, for instance, on paratype 5617.

On the other hand, there seems to be a difference in the spacing of septa in mature individuals of the two forms. In *G. goniolobum* the septa in late mature volutions are spaced nearly twice as closely as they are in *G. welleri* at the same stage of growth. This is not incidental local crowding of septa, as occasionally observed near the living chamber of mature or senile ammonoids; the dense spacing of sutures is shown to be quite uniform on the drawing of the original *G. goniolobum* and is mentioned in Meek's description; the specimens of this species from Kansas also show the same uniformity in close spacing of the sutures.

Summarizing these observations, *G. welleri* differs from *G. goniolobum* in having a flattened and somewhat narrower venter and in having less crowded septa in late maturity. The distinction in the

spacing of septa becomes less conspicuous and the difference in shape of the conch disappears completely in early adolescent and still younger volutions. The wider spacing of septa has been observed by me on only three mature specimens of *G. welleri*, all of which came from the Wayland shale of Texas. It is important that one of these is among the types in Smith's collection. This is the original of his pl. 21, fig. 3 (5898, Stanford Univ. coll.), two photographs and a drawing of the sutures of which are here reproduced (pl. 19, figs. 1a, 1b, and fig. D). Because Smith did not designate which of his cotypes is the holotype, I indicate this mature specimen as holotype of *G. welleri* by subsequent designation. Only through selection of this wholly mature specimen for holotype is it possible to continue to regard *G. welleri* as a separate species from *G. goniolobum* without creating confusion.

In the examined collection of Smith's types from Stanford University, immature specimen 5616 is labeled as holotype, which selection, however, may be disregarded even if it was made by Smith himself, because neither Smith nor anyone else has ever published it.

Unless this late mature specimen is considered to represent typical *G. welleri*, the only distinctive features by which it may be conveniently differentiated from *G. goniolobum*—the difference in spacing of septa and the flattened, not rounded, venter—will disappear from consideration, because the early mature and still younger volutions of *G. welleri* and *G. goniolobum* have their sutures spaced more nearly alike and show no difference in shape of venter. Examination of the external sutures on three mature volutions of *G. welleri* and on volutions of corresponding diameter of the holotype of *G. goniolobum* (on Meek's sketch) and of two specimens from Kansas in the University of Kansas collection permits the following conclusions:

The difference in spacing of sutures between *G. welleri* and *G. goniolobum* becomes distinct when radius of volutions reaches about 39 to 40 mm., or when the distance from the apex of the second lateral lobe to the venter becomes about 20 mm. (This distance can be conveniently measured on the many fragments that lack umbilical region.) At this radius the distance between the sutures measured across about the middle of the lines on either side of the first lateral saddle is 1.5 to 2 mm. in *G. goniolobum* and about 3 mm. in *G. welleri*.

If the two forms are specifically different, they seem also to belong to somewhat different horizons. *G. goniolobum* has been found in Kansas only in the Kansas City group of the Missouri series. In the higher Virgil series only young individuals referable either to *G. goniolobum* or to *G. welleri* have been collected. The Wayland shale, from the Graham of the Cisco of Texas, where *G. welleri* is found in great abundance, is undoubtedly stratigraphically higher than the Missouri series of Kansas and probably corresponds to the uppermost Shawnee group of the Virgil series of Kansas. This conclusion is based on the detailed comparison of Kansas and Texas fusulinids and some fenestrate bryozoans (2).

Occurrence.—Wayland shale of the Graham formation, Cisco group, near Graham, Texas; young individuals in large concretions in the shale above Elmo coal, Cedar Vale shale, 2 miles west and 3 miles south of Burlington Junction, Nodaway County, Mo.; shale interval of Dover limestone 1 mile north and 1½ miles east of Piedmont, Kans., and in shale interval of Grandhaven limestone (next above the Dover), at northern end of Emporia, Kans. All occurrences in Kansas are from the lower part of the Wabaunsee group, Virgil series. Only small individuals were collected from localities in Kansas, and in view of similarity of the young of *G. welleri* and *G. goniolobum* they may be referable to either of these two species.

GONIOLOBOCERAS GONIOLOBUM (Meek)

Plate 20, figures 1–3b and text figure 1, L to M^8

Goniatites goniolobum MEEK, *1877*, U. S. Geol. Expl. 40th Par. Rept., vol. 4, pt. 1, p. 98, pl. 9, figs. 5, 5a, 5b.

Goniatites sp. KEYES, *1894*, Missouri Geol. Survey, vol. 5, pl. 56, fig. 1.

Goniatites parrishi MILLER and GURLEY, *1896*, Illinois State Mus. Nat. History Bull. 11, p. 36, pl. 4, figs. 6–8.

Gonioloboceras goniolobum SMITH, *1903*, Carboniferous ammonoids of America: U. S. Geol. Survey Mon. 42, pp. 123–124, pl. 4, figs. 1–3 (same figures as published by Meek).—SAYRE, *1930*, Fauna of the Drum limestone of Kansas and western Missouri, Kansas Univ. Sci. Bull., vol. 19, p. 157, pl. 21, fig. 5 (×⅔).

Milleroceras parrishi SMITH, *1903*, Idem, pp. 127–128, pl. 16, figs. 6–8.—MILLER, *1932*, Jour. Paleontology, vol. 6, pp. 72–73, pl. 12, figs. 5–7.

Milleroceras minusculum MILLER, *1932*, Idem, pp. 73–76, pl. 12, figs. 8, 11.

Gurleyoceras discoidale (Böse), MILLER, *1932*, Idem, pp. 77–79, pl. 12, figs. 14–16.

Goniolaboceras gracellenae MILLER and CLINE, *1934*, Jour. Paleontology, vol. 8, pp. 175–176, pl. 28, figs. 14–18.

As the type of this species is lost, only its figures and description by Meek are available for comparison with the newly collected material. The specimen from the Drum limestone from Kansas City, Mo., described by Sayre as *G. goniolobum* has been examined by me, and I agree with Sayre's identification. I collected another specimen of the species from the oolitic Westerville limestone 2 miles northeast of Welborn (west of Kansas City), Kans., on which I was able to study juvenile stages. I found that juvenile stages of *G. goniolobum* and *G. welleri* are so similar that the two can hardly be distinguished. Only in the much advanced volutions, with radii greater than about 3 cm (diameter about 5 cm), can the two species possibly be recognized. I conclude furthermore that both *G. goniolobum* and *G. welleri* in their earliest stages are identical with what Hyatt considered as *Milleroceras parrishi*, which is the genotype of *Milleroceras*. I agree with J. P. Smith (13, pp. 127–128), who doubted the validity of this genus and with G. H. Girty (3, p. 261), who considered it a synonym of *Goniolaboceras*.

I suggest that the term milleroceran be used only as a stage name for certain juvenile specimens of *Goniolaboceras*. Thus I would say, for instance, that in the prolific collection of small ammonoids from the Dover and Grandhaven formations at Piedmont and at Emporia, Kans., respectively, *Goniolaboceras* is represented exclusively by juvenile individuals in glyphioceran and, rarely, milleroceran stages of development. The milleroceran stage may be characterized by its inflated conch nearly elliptical in cross section (platycone), and its suture with angular and pointed lateral lobes and subangular and nonpointed lateral saddles. The first lateral saddle becomes pointed when it attains a diameter of about 18 mm, radius 10 mm, when the milleroceran stage changes to goniolaboceran. The glyphioceran stage was observed by me on early volutions of *G. goniolobum* from the oolitic Westerville limestone northwest of Kansas City, Kans. Both these stages seem to be indistinguishable from the corresponding stages of *G. welleri* except by wider spacing of sutures in the latter (compare text fig. 1, G to J^1 with M^2 and M^3). The similarity extends also to the early mature volutions of the two species with typical goniolaboceran suture, until a diameter of about 5 cm is reached. In larger volutions the conch becomes somewhat more rounded on the sides and at the venter than in *G. welleri*, and the sutures seem to be more closely spaced. Otherwise *G. goniolobum* can be characterized in exactly the same way as *G. welleri* (see description of the conch, lines of growth, and suture of the latter on p. 95).

By breaking the specimen of *G. goniolobum* from the Westerville (?) I was able to observe a stage of its development earlier than glyphioceran. This earliest stage of *G. goniolobum* is observed on its first volution, the conch of which is a cadicone about 1 mm thick. The external suture has only one lateral

saddle and one lateral lobe on each side. The ventral saddle is very low and is not dented at the apex.

Occurrence.—Upper Pennsylvanian of New Mexico (original).

Ammonoid beds in sandstone (Abo?), 1¼ miles east of Tularosa, N. Mex., yielded only juvenile forms, (6) which probably belong to *G. goniolobocerας* and not to *G. welleri*. Westerville and Raytown (?) limestones of the Kansas City group, Missouri series, at Kansas City, Mo., and at Kansas City, Kans. At the top of the Raytown of Iola limestone, Kansas City group, Missouri series, at Iola, Kans. (collected by J. M. Jewett).

Genus GONIOGLYPHIOCERAS Plummer and Scott, 1937

Goniolobocerας welleri var. *gracile*, which was described by Girty from the Wewoka of Oklahoma, differs from *G. welleri* not only in its angular venter, which is provided with a narrow ventral groove (no ventral groove exists, as is here demonstrated, in *G. welleri*), but also in rounded instead of angular apices of the lateral saddle and lateral lobes. These distinctive features are important enough to warrant not only specific, as correctly suggested by A. K. Miller (6), but also generic separation of *gracile* from *Goniolobocerας welleri*. Form *gracile* differs from this and other species of *Goniolobocerας* (*G. goniolobum*) more than *Milleroceras* (now considered a synonym of *Goniolobocerας*) and it can not be retained in *Goniolobocerας* unless the diagnosis of the latter genus is profoundly modified. For this form Plummer and Scott proposed a new generic name *Gonioglyphioceras*.

In form of conch *Gonioglyphioceras* resembles the much older *Sagittoceras*, to which this genus and *Goniolobocerας* are undoubtedly related. Comparison of American and European representatives of these genera was a special subject of a recent paper by A. K. Miller (7), and therefore a brief discussion in regard to the particular difference between *Gonioglyphioceras* and *Saggittoceras* will be sufficient. Judging from descriptions and illustrations, *Sagittoceras* does not possess a ventral channel "guarded by two thin angular ridges," which is so typical of *Gonioglyphioceras gracile*. A still more important distinction, which, in the spirit of the modern tendency of finer generic splitting of Glyphioceratidae, is undoubtedly of generic rank, is the rounded lateral lobes of *Gonioglyphioceras* in contrast with the sharply ended tips of the same lobes in *Sagittoceras*. It may be added that *Sagittoceras* belongs to the Namurian and still older rocks of the Carboniferous whereas *Gonioglyphioceras* has been found in rocks that correspond to the upper Westphalian and precisely, as I correlate, to the lower part of the Westphalian D (= Radstockian) of Europe.

It comes from the Wewoka shale of Oklahoma, which is correlated with the lower part of the Marmaton group, Des Moines series, of Kansas and Missouri. This correlation is substantiated by the latest stratigraphic studies in Oklahoma and southeastern Kansas by Dr. N. D. Newell of the University of Kansas. The species of *Goniolobocerας* belong to still higher beds of the Pennsylvanian.

GONIOGLYPHIOCERAS GRACILE (Girty)

Plate 20, figures 7a, 7b; text figure 1, N to O²

Goniolobocerας welleri var. *gracile* GIRTY, *1911*, New York Acad. Sci. Annals, vol. 21, p. 153; *1915*, Fauna of the Wewoka formation of Oklahoma, U. S. Geol. Survey Bull. 544, pp. 263–264, pl. 35, figs. 3–5b.

Gurleyoceras gracile MILLER, *1932*, Pennsylvanian cephalopod fauna from south-central New Mexico, Jour. Paleontology, vol. 6, p. 76.

Gonioglypioceras gracile PLUMMER and SCOTT, *1937*, Mississippian, Pennsylvanian and Permian ammonoids of Texas, Texas Univ. Bull. 3701, pp. 337.

The very accurate description of the species by Girty is as follows:

> This species shows a diameter of 53 mm in a fragment entirely septate, but the type specimen has a diameter of 43 mm, and its thickness through the center is 14 mm. The umbilicus is small, only 3 mm wide, and the whorls are highly involute. The sides are gently convex, contracting to a very narrow

venter marked by a revolving channel guarded by two thin, angular ridges. In the early stages the shell is less compressed and the venter less distinctly channeled. When still younger the venter was probably rounded, but the two carinae with their inclosed groove are largely a development of the test and do not show clearly on the internal mold. The surface appears to be marked by obscure, incremental lirae, the direction of which indicates a deep, broad, hyponomic sinus.

The suture consists of two lobes and two saddles on each side, together with a high, broad siphonal saddle, which is rounded, but has a notch on the median line. The latter feature is not clear. The suture lines bend sharply backward near the middle, but in most specimens they appear to be disconnected. In one, however, they appear to connect into a small V-shaped reentrant angle. The second saddle is broad and asymmetric. The first saddle and the two adjacent lobes are very nearly equal, the second lobe being slightly broader. They are subangular but not acutely pointed. The sutures are closely arranged, the inner sides of the first saddles being almost in contact.

In view of the considerable change in the conception of *G. welleri* as here revised, the comparison with it, as expressed by Girty in 1915, must also be revised. *G. gracile* differs from *G. welleri* and from *G. goniolobum* in having a much narrower venter and nonpointed lateral saddles and lobes not only on juvenile but also on mature individuals. Furthermore the conch of *G. gracile* has a ventral channel guarded by two thin low angular ridges, whereas the venter of the conch in both *G. welleri* and *G. goniolobum* is smooth.

Occurrence.—Lower shaly members of Wewoka formation (corresponding to the lower part of the Marmaton group of Kansas), Des Moines series, along Canadian River in T. 5 N., R. 8 E., and Tps. 6 and 7 N., R. 9 E., Oklahoma.

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III. *PROPERRINITES PLUMMERI* ELIAS, N. GEN AND SP., FROM LATE PALEOZOIC ROCKS OF KANSAS

ABSTRACT

In structure and in stratigraphic position the new genus *Properrinites* is intermediate between *Shumardites* and *Perrinites*. *Properrinites plummeri*, n. sp., from the Neva limestone of the Big Blue series in Kansas is an intermediate form between *Shumardites simondsi* Smith and *Properrinites bösei* (Plummer and Scott).

Among the fossils collected in the early days of geologic activities in Kansas is an ammonoid (collected by West) that is of considerable importance for exact correlation of the late Paleozoic rocks of Kansas and Texas. The prolific ammonoid faunas of Texas allowed F. B. Plummer and Gayle Scott (6) to construct several phylogenetic series.

With the help of the phylogenetic series it became possible to establish the exact genetic relationship of the specimen from Kansas here described as *Properrinites plummeri* to the forms from Texas, and through this to project its horizon upon the composite geologic section of north-central Texas.

Group of *Shumardites-Perrinites*

Since the genotype of *Shumardites* was described by Smith (10, pp. 134–138) this genus has been considered to represent a probable ancestor of the supposed primitive *Waagenoceras* from the Wichita group of Texas, which is now known under the name *Perrinites cumminsi* (White). This conclusion is based on the remarkable similarity in construction of the septa in *Shumardites* and *Perrinites*, which increase in complexity very gradually with the advance of geologic age, and the conch, which does not change much but remains inflated and elliptical in cross section (platycone) with only slightly greater lateral compression in stratigraphically higher forms. Complete discussion of the suture and other characters of the genus *Shumardites* is given in the papers by Smith (10, pp. 134–138), Miller and Cline (4, pp. 183–185), and Plummer and Scott (6, pp. 294–297). For the purpose of this discussion it is sufficient to point out that there is one important peculiarity in the suture of *Shumardites* that is not repeated in the suture of *Perrinites:* this is the grouping of the three lateral lobes in such a way that the middle lobe is lower than the two adjacent lobes and all three are constructed symmetrically about the central line of this middle lobe. Smith, who noticed this construction of the suture in *Shumardites*, remarks in his description of the genotype that these

> lateral lobes are secondary, and have developed out of a single primary lobe; this is borne out by the ontogeny of the species.

His illustrations of the ontogeny of the suture of *S. simondsi* show this development excellently (10, pl. 3, figs. 7–11). Almost nothing suggestive of such grouping of the first three lateral lobes into a natural symmetrical set can be detected on sutures of *Perrinites* (*Waagenoceras*) *cumminsi* (White) and of still more advanced species of *Perrinites*, but traces of symmetrical arrangement of the three lobes can be distinctly seen on the more primitive *Properrinites bösei* illustrated by Plummer and Scott in Sellards (5, pl. 6) and on *Properrinites plummeri* Elias, here described.

Genus PROPERRINITES Elias, n. gen.

Genotype: *Properrinites plummeri* Elias

Properrinites has an inflated elliptical conch (platycone) as in *Shumardites* and *Perrinites* and a suture that is intermediate between the sutures of these two genera. Ventral lobe is large and is divided by a siphonal saddle, the upper part of which is more inflated than that in *Shumardites* and the lower part of which is less dissected than that in *Perrinites*. The first three lateral lobes show gradual decrease in size as do those in *Perrinites*, but their dissection is symmetrical about the middle (second) lobe, as in *Shumardites*. In intensity of dissection of the suture *Properrinites* is intermediate between *Shumardites* and *Perrinites*. The two branches of the ventral lobe have three notches each, but the same halves of the ventral lobe in the most advanced *Shumardites simondsi* have only two notches, and those of the most primitive *Perrinites cumminsi* have four notches. The lateral saddles of *Properrinites* have conspicuously inflated apices, which are separated from the bodies of the saddles by a necklike contraction. The apices of the lateral saddles in *Shumardites* are only very slightly inflated. The corresponding apices of the saddles in *Perrinites* are much dissected, and what is a single inflated apex in *Properrinites* is here divided by a wide adoral notch into two unequal halves. The number of lateral lobes and saddles in the external suture of *Properrinites* is the same as in *Shumardites simondsi*—four lateral lobes and four saddles—in addition to which a fifth saddle is developed on the umbilical shoulder. This observation is made on the suture of *Properrinites bösei* illustrated by Plummer and Scott; the specimen of *Properrinites plummeri* from Kansas is incomplete, lacking the umbilicus.

In contrast with *Shumardites* and *Properrinites*, the external suture of *Perrinites cumminsi* has six lateral saddles and five lobes. The internal suture of *Properrinites plummeri* is poorly preserved and that of *Properrinites bösei* has not been described or illustrated. Because it is represented by a more complete specimen, *Properrinites bösei* is selected as the genotype of *Properrinites*.

No member of the *Shumardites-Perrinites* group has been found outside of North America. *Godthaabites freeboldi* from the Lower Permian of Greenland has been compared by its originator (3, pp. 17–21) to an intermediate genus between *Shumardites* and *Perrinites*, but this relationship seems to be highly problematic and is not supported by ontogenetic study of *Godthaabites*. The siphonal saddle of *Godthaabites*, if correctly illustrated (3, fig. 3, p. 20, second from top), is very low and not at all like the typical prominent siphonal saddle of *Shumardites*, *Properrinites*, and *Perrinites*. Furthermore, all four lateral lobes of *Godthaabites* are symmetrically trifid, with a sharp and comparatively long central secondary lobe in each. This is very unlike the character of subdivision of the lateral lobes in *Shumardites* and *Properrinites*, in which the first and third lateral lobes are asymmetrical and are unlike the symmetrical second lobe. In the character of its lateral saddles and lobes *Godthaabites* is more like *Marathonites* than *Shumardites* or *Properrinites*. After this was written I learned through Dr. A. K. Miller that O. H. Schindewolf had published the same conclusion in regard to *Godthaabites*. Very recently Ružencev (8, pp. 487, 488, 496, 503) recorded from the Artinskian and underlying Sakmarian rocks of southern Urals some ammonoids for which he proposes a new generic name *Neoshumardites*. The subsequent description of the genus by Ružencev (8, pp. 1084, 1085, 1088) leaves no doubt that this genus is quite unlike *Properrinites* and represents an independent line of ascent from the lower Carboniferous *Proshumardites* Rauser (7 pp. 165–167, pl. 1, figs. 1, 2), retaining the primitive character of the external part of the suture, as in the latter genus, but developing tripartite division of the internal lobes.

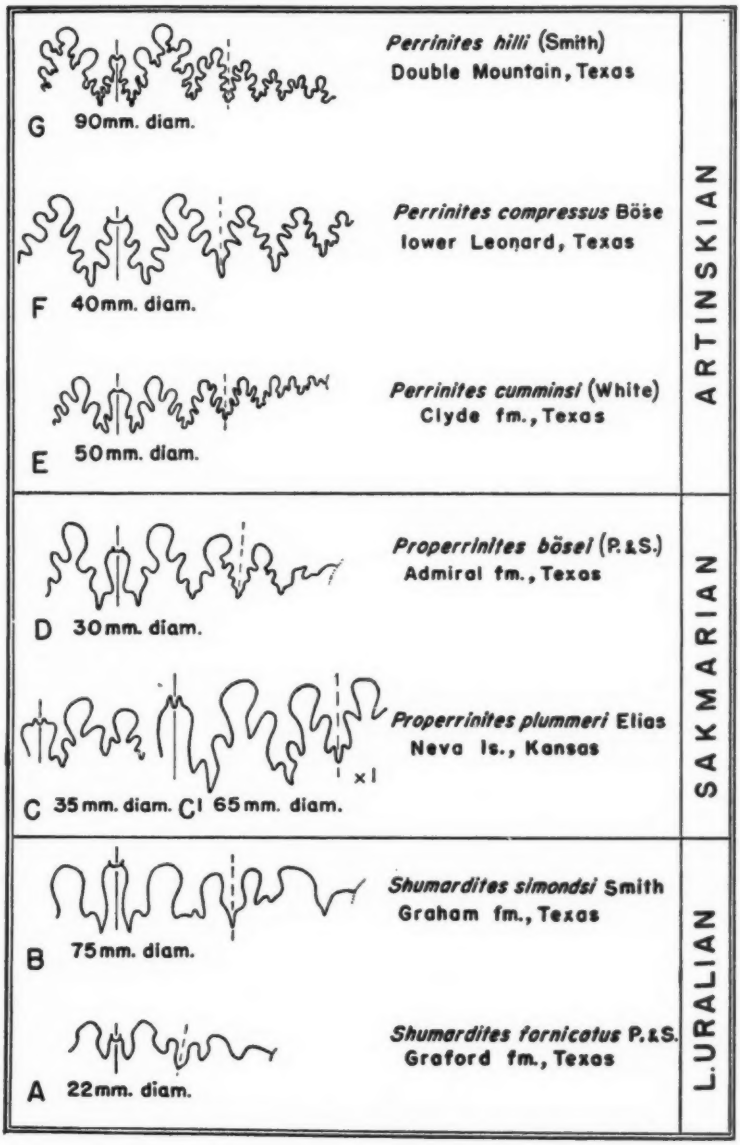

FIG. 2—*Shumardites-Perrinites* evolutionary series, modified after F. B. Plummer (1932, plate 6, opp. p. 238), with the addition of *Properrinites plummeri* Elias from Kansas, the suture lines of which are shown in *C* and C^1. The lower part of the Big Blue series of Kansas and the Admiral formation of Texas are correlated with the Sakmarian or uppermost Uralian of Urals, and the upper Wichita (Belle Plains and Clyde) is correlated with the Artinskian.

PROPERRINITES PLUMMERI
Elias, n. sp.

Plate 20, figures 8, 8a and text figures 2 C, C[1]

Perrinites aff. *P. bösei*, ELIAS, *1936*, 16th Internat. Geol. Cong. Rept., p. 694.

The single specimen of the species is a fragment of internal mold in somewhat weathered yellowish-white limestone with numerous molds of small pelecypods. The mold has a smooth surface without constrictions and belongs to an ellipsocone. The conch itself is not preserved and, therefore, its sculpture remains unknown. An inner whorl has been broken off for study. The somewhat weathered surface of this fragment discloses no traces of the external sculpture of the weathered or dissolved shell, which must have been very thin and apparently without pronounced sculpture. The external sutures of the fragment taken on its external and internal volutions are shown in figures 1C and C[1]. Their general features have been discussed in the generic description of *Properrinites*. The suture of *P. plummeri* differs from that of *P. bösei* by the lesser dissection of saddles and lobes, the differences being best observed on volutions of comparable diameter, as in sutures of *P. bösei* at a diameter of 30 mm. and of *P. plummeri* at a diameter of 35 mm. At these sizes, the first lateral lobe of *P. bösei* has 5 incisions as compared with 3 of *P. plummeri*. The corresponding lateral lobe of *P. plummeri* at a diameter of 65 mm. is much closer to that of *P. bösei* at a diameter of 30 mm., but the second lateral lobe of *P. plummeri* even at the large diameter of 65 mm. has only five incisions whereas the corresponding lobe of *P. bösei* at much smaller size (30 mm.) has 8 incisions.

The internal sutures of *P. plummeri* are so crowded and so weathered on the specimen from Kansas that they cannot be illustrated with any reasonable degree of accuracy. They are generally comparable with those of *Schumardites* and *Perrinites*. The species is named after Dr. F. B. Plummer of the University of Texas, who is responsible for the construction of the evolutionary series of *Schumardites-Perrinites*.

Occurrence.—The single specimen of *P. plummeri* came from a locality east of Beaumont, Kansas. Only the rocks of the lower part of the Big Blue series from the Foraker to the Florence are here exposed. The comparison of the matrix full of molds of small pelecypods with the exposed rocks at Beaumont permits one to conclude that the specimen came most probably from the uppermost layer of the Neva limestone, where mollusks of this type are very common. Special search for cephalopods in this zone yielded only a few straight-shelled nautiloids, but cephalopods in general and ammonoids in particular are usually found only sporadically in the late Paleozoic rocks of Kansas. Special search for ammonoids during the past few years by me and other collectors shows that excepting immature individuals, which are common at a few horizons in the Virgil series, one very seldom is able to collect more than one or two individuals of ammonoids at a single horizon and locality even after a very careful and determined search.

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NEW TERTIARY MOLLUSKS FROM WESTERN NORTH AMERICA

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ABSTRACT

Two new pelecypods and three new gastropods from the Miocene of California and one new gastropod from the Oligocene of Washington are described and figured. A new name, *Natica teglandi* Hanna and Hertlein, is proposed for *N. dalli* Tegland, which is preoccupied.

While engaged in a study of certain groups of western American Tertiary and Recent mollusks in the collection of the California Academy of Sciences, the authors found several species that do not appear to have been recorded heretofore. Several of the fossils are of considerable importance in stratigraphic work in progress, in which reference to them is necessary. The purpose of the present paper is to describe these forms. The photographs were made by Mr. Frank L. Rogers.

Genus MYTILUS Linnaeus, 1758

MYTILUS SCHENCKI Hanna and Hertlein, n. sp.

Plate 21, figure 11

Shell rather flat with the anterior part somewhat constricted, curved, but very broadly rounded and expanded posteriorly. Length (incomplete), about 138 mm.

The broad expanded posterior part of this species is quite distinct from any of the described species from western America, such as *M. expansus* Arnold (1) and *M. loeli* Grant (2) from the Vaqueros of California. Arnold's species bears a decided resemblance to *M. aquitanicus* Mayer (3). Somewhat the same general shape of the new species seems to be indicated in the figure of the type of *M vancouverensis* Clark and Arnold (4) but it appears to be much less expanded.

The species is named for Dr. Hubert G. Schenck, Professor of Paleontology of Stanford University, who has very kindly presented the type specimen to us and who has coöperated with us in many other ways.

Type.—Holotype (California Acad. Sci. Paleont. Type. Coll. 4686), from upper part of Vineyard Canyon in the Southwest corner of the NW ¼ SW ¼ sec. 23, T. 23 S., R. 13 E., Mount Diablo Base and Meridian, San Miguel quadrangle, Calif. N. L. Taliaferro, collector. ?Santa Margarita formation, upper Miocene.

Genus MACOMA Leach, 1819

MACOMA MENKENI Hanna and Hertlein, n. sp.

Plate 21, figures 1 and 2

Shell subcircular; slightly projecting posteriorly with an angulation running from the beak to the ventral margin, the posterior margin of the shell sloping rapidly downward, and a broad gentle depression anterior to the fold causing a slanting bend in the lines of growth; beaks about two-fifths the distance from the anterior end. Length, 41 mm.; height (beak to base), 34 mm.

Macoma menkeni has a much more rounded outline, and the beaks are more anteriorly placed than in the Recent *M.*

secta (Conrad) (5). The same characters separate it from *M. panzana* Wiedey (6) described from the Miocene and *M. inquinata affinis* Nomland (7) from the Pliocene.

The species is named for Mr. F. A. Menken, Chief Geologist of the Associated Oil Co., who has contributed many important collections of fossils to the Academy and has made it possible to greatly enlarge its scope of inquiry.

Type.—Holotype (California Acad. Sci. Paleont. Type Coll. 6900, right valve), and paratype (6901, left valve) from locality 28,682 (Calif. Acad. Sci.), Chancellor Canfield Midway Oil Co., well no. 7, sec. 6, T. 28 S., R. 29 E., Mount Diablo Base and Meridian, Kern County, Calif., at a depth of 1,223 to 1,240 feet. Temblor, Miocene.

Genus MEGASURCULA Casey, 1904

MEGASURCULA HOWEI Hanna and Hertlein, n. sp.
Plate 21, figures 10, 12, 13

Shell biconic, whorls with angulation about two-thirds the distance up the body whorl, ornamented by a row of 12 rounded nodes; on the upper whorls the nodes are covered and obscured by the succeeding whorl so that the spire is smooth, flat and conic; body whorl below the angulation moderately rounded; surface of shell covered by fine spiral lines, which are stronger toward the base of the body whorl. A shallow siphonal fasciole on the type specimen. Posterior notch slight and marked by gently rounded lines of growth. Length (incomplete), 53 mm.; greatest width, 28 mm.

Megesurcula howei differs from *M. keepi* (Arnold) (8) also from the Temblor, Miocene, and from the Recent *M. tryoniana* (Gabb) (9) in that the spire of the new species is flat-sided and conical and the nodes on the angulation of the earlier whorls are covered with shell material. On *keepi* the surface above the angulation is concavely rounded and the suture does not reach to the nodes, which are visible on Arnold's figure even on the early whorls. The lower smooth conic spire separates the new species from *M. tryoniana*, which has been recorded from Pliocene to Recent. The remarks of Grant and Gale (10) regarding *keepi* seem applicable to the species here described but not to the species represented in Arnold's figure. *M. condonana* (Anderson and Martin) (11) from the Miocene near Yaquina, Oregon, possesses concavely rounded whorls and heavier sculpture than *M. howei*.

The species is named for Dr. Henry V. Howe, Secretary of the Society of Economic Paleontologists and Mineralogists and Professor of Paleontology at the University of Louisiana, who, while working on the Oregon Tertiary, first noted that this species was undescribed.

Type.—Holotype (California Acad. Sci. Paleont. Type Coll. 7082) from locality 64 (Calif. Acad. Sci.), in the bed of a small gulch about 1¼ miles northeast of Barker's ranch house on Kern River, Kern County, Calif.; F. M. Anderson and Bruce Martin, collectors. Temblor, Miocene. Paratype (California Acad. Sci. Paleont. Type Coll. 7083) from locality 65 (Calif. Acad. Sci.), from hills just north of Kern River and northeast of Barker's ranch house, Kern County, Calif.; F. M. Anderson and Bruce Martin, collectors. Temblor, Miocene.

Genus NATICA Scopoli, 1777

NATICA POSUNCULA Hanna and Hertlein, n. sp.
Plate 21, figure 6

Shell ovate, spire moderately low; whorls 3½, broadly rounded, smooth except for fine lines of growth; outer lip thin, inner lip with a moderate callus; umbilical opening semicircular and about three-eighths closed by a well-developed funicle, above which there is a decided indentation in the callus. Height, 22.4 mm.; maximum diameter, 20.8 mm.; length of aperture, 17.8 mm.

Natica posuncula bears a resemblance to *Natica catenata* Philippi (12) but has a decidedly lower spire and less strongly

developed subsutural axial riblets, which are particularly pronounced on the upper part of the spire of *N. catenata*. *Natica teglandi* Hanna and Hertlein (13) is similar to the new species but it appears to be heavier, and is described as having a well-developed shoulder and slightly flattened whorls.

Posuncula is the original name for Kern River.

Type.—Holotype (California Acad. Sci. Paleont. Type Coll. 7084) and paratypes (7085 and 7086) from locality 65 (Calif. Acad. Sci.), from hills just north of Kern River and northeast of Barker's ranch house, Kern County, Calif. F. M. Anderson and B. Martin, collectors. Temblor, Miocene.

NATICA TEGLANDI Hanna and Hertlein, n. name

Natica (*Natica*) *dalli* TEGLAND (not Cossmann), *1933*, Univ. Calif. Dept. Geol. Sci., Bull., vol. 23, no. 3, p. 138, pl. 14, figs. 8–12.

The name *Natica teglandi* is here proposed to replace *N. dalli* Tegland, which specific name was used by Cossmann (14) in 1925 as a substitute for *N. consors* Dall, from the Empire formation of Coos Bay, Oregon. The type of *N. teglandi* is from Blakeley, Wash.

Genus CERITHIUM Bruguière, 1789

CERITHIUM BARBATI Hanna and Hertlein, n. sp.

Plate 21, figures 7, 8, 9

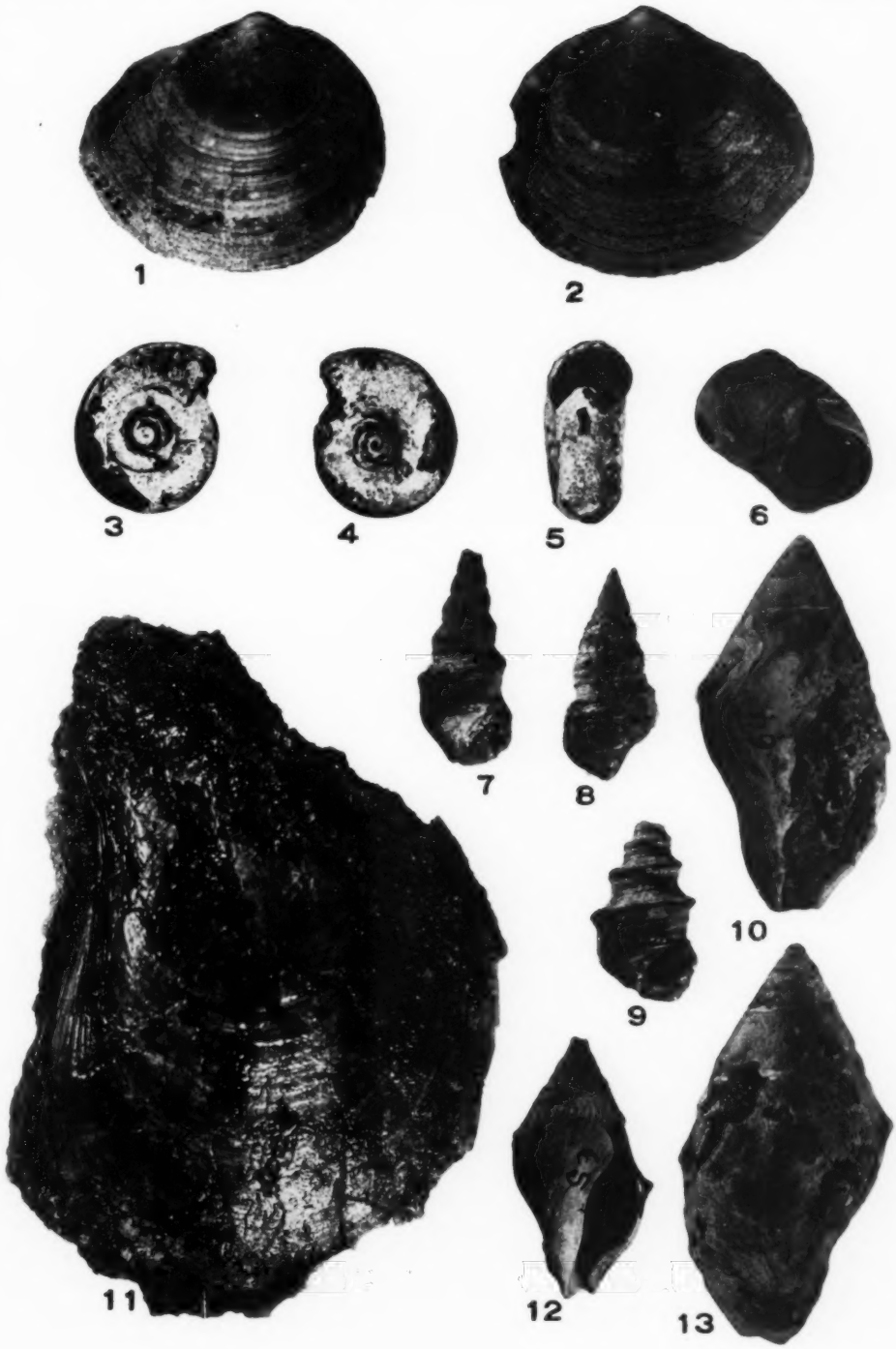
Holotype with 5½ whorls, the last 2½ with a sharply angulated shoulder bearing a heavy carina; apex and a small part of peristome missing; upper three whorls strongly cancellated, the third with about 18 axial ribs crossed by 8 spiral threads; this sculpture merges gradually into that of the later whorls, marked only by spiral threads of very irregular strength and disposition and the heavy carina on the shoulder; between the termination of the outer lip and the shoulder there are 10 of these spirals roughly arranged in pairs; aperture rather small and canal (partly broken) apparently short and recurved slightly; parietal wall covered with a heavy callus. Length, 17.5 mm.; diameter, 7.9 mm.

One of the paratypes (fig. 8) shows that the cancellated sculpture extends to the apex, which is complete; this shell is about the same size as the type and contains eight whorls; the axial ribs are very nearly in line from whorl to whorl, and there are only six spirals on the whorl immediately preceding the carina. Another paratype (fig. 9) has the carina extremely developed, thus giving the shell an appearance of shortness in proportion to diameter; in the lot available for study there seemed to be sufficient specimens intergrading between the extremes illustrated by the two paratypes to warrant the assumption that only one highly variable species is present.

The very strong carina easily separates *C. barbati* from other species of the genus cited from the Temblor forma-

EXPLANATION OF PLATE 21

FIG. *1*—*Macoma menkeni* Hanna and Hertlein, n. sp. Holotype, right valve (6900).
2—*Macoma menkeni* Hanna and Hertlein, n. sp. Paratype, left valve (6901).
3—*Segmentina durhami* Hanna and Hertlein, n. sp. Dorsal view of the holotype (5620).
4—*Segmentina durhami* Hanna and Hertlein, n. sp. Ventral view of the holotype.
5—*Segmentina durhami* Hanna and Hertlein, n. sp. Apertural view of the holotype.
6—*Natica posuncula* Hanna and Hertlein, n. sp. Holotype (7084).
7—*Cerithium barbati* Hanna and Hertlein, n. sp. Holotype (7091).
8—*Cerithium barbati* Hanna and Hertlein, n. sp. Paratype (7092).
9—*Cerithium barbati* Hanna and Hertlein, n. sp. Paratype (7093).
10—*Megasurcula howei* Hanna and Hertlein, n. sp. Holotype (7082).
11—*Mytilus schencki* Hanna and Hertlein, n. sp. Holotype (4686).
12—*Megasurcula howei* Hanna and Hertlein, n. sp. Paratype (7083).
13—*Megasurcula howei* Hanna and Hertlein, n. sp. Another view of the holotype shown in figure 10.



Hanna and Hertlein, Tertiary Mollusks

UNIV. OF MICH.

tion, such as *C. topangensis* Arnold (15) and *C. arnoldi* Anderson and Martin (16). The carinated whorls resemble somewhat those of *Terebra santana* Loel and Corey.

The species is named for the collector, Mr. William Barbat, who, through the Standard Oil Co. of California, has supplied the Academy with many important collections of fossils.

Type.—Holotype (California Acad. Sci. Paleont. Type Coll. 7091) and paratypes (7092 and 7093), from locality 25,704 (Calif. Acad. Sci.), NE¼ sec. 22, T. 25 S., R. 16 E., Mount Diablo Base and Meridian; W. Barbat, collector. Temblor, Miocene

Genus SEGMENTINA Fleming, 1818

SEGMENTINA DURHAMI Hanna and Hertlein, n. sp.
Plate 21, figures 3, 4, 5

Shell large for the genus, consisting of 4½ whorls, evenly rounded on the periphery and very obtusely, roundly angulated above and below; sculpture fine, evenly spaced riblets or growth ridges; first 3½ whorls of spire almost flat; last whorl slightly elevated above this plane, all regularly increasing in size; umbilicus broadly and evenly concave; the outside of the body whorl is largely stripped of shell material, but a short distance back of the termination there are three short, spiral, slightly descending ridges of callus embedded in the matrix; these are believed to be the remains of the apertural teeth, so characteristic of the genus; the lower one of these crosses the periphery. Greatest diameter, 12 mm.; height, 5.2 mm.

The shape is strongly indicative of the genus *Segmentina* and very similar to *S. armigera* (Say) (17) although about twice as large for the same number of whorls. The aperture is missing, but the slightly descending remains of what seem to have been lamellae make the generic assignment reasonably certain.

Type.—Holotype (California Acad.Sci Paleont. Type Coll. 5620) from a locality a quarter of a mile north of Woodman's station on shore of Port Discovery Bay in sec. 5, T. 29 N., R. 1 W., western Washington; J. Wyatt Durham, collector. Oligocene.

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BOTHRIOLEPIS STENSIÖI, A NEW DEVONIAN PLACODERM FROM GASPÉ, CANADA

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ABSTRACT

A well-preserved cephalic shield from the Escuminac formation on the north shore of Chaleur Bay, opposite Dalhousie, is described and figured.

In September, 1934, accompanied by C. H. Kindle and G. F. Adams of the Department of Geology, City College of New York, the author collected placoderm remains on the north shore of Chaleur Bay opposite Dalhousie, west of the Maguasha pier. The remains occur in sandstone concretions from the Escuminac formation. One specimen, a cephalic shield, upon examination proved to be an undescribed species of *Bothriolepis*.

F. J. Alcock (1935) lists two species of *Bothriolepis*, *B. canadensis* Whiteaves and *B. traquairi* Bryant from the Escuminac formation of this locality. W. L. Bryant (1924) bases his species on a ventral shield, the only recorded specimen of that locality.

The author wishes to acknowledge his gratitude to Drs. H. N. Coryell, W. K. Gregory, and C. H. Kindle for their advice and encouragement, and to G. F. Adams for the invitation to accompany Doctor Kindle and him to Gaspé.

Genus BOTHRIOLEPIS Eichwald, 1840

Bothriolepis EICHWALD, *1840*, Acad. imp. Sci., St. Petrsbrg., Bull. sci., vol. 7, p. 79.—TRAQUAIR, *1888*, Ann. and Mag. Nat. History, ser. 6, vol. 2, p. 497, pl. 18, fig. 6.—STENSIÖ, *1931*, Meddelelser om Grönland, bind 81, no. 1, p. 161, text fig. 74.

R. H. Traquair (1888) gives the following description of the cephalic sensory canal system of *Bothriolepis:*

> The pattern of the cephalic lateral-line grooves is considerably different from that of *Asterolepis* and *Pterichthys*. No transverse commissure unites the lateral grooves of each side across the occipital plates, as in those genera: but in front, just at its inward flexure on the lateral plate, a conspicuous branch is given off, which runs forwards and outwards to the margin of the shield, while immediately behind the origin of this branch and on the inner side of the main groove a small ear-shaped mark is often, though not always, seen. On the median occipital two slighter grooves are seen, forming an angle with each other behind, whence, diverging obliquely forwards and outwards, they pass also over the lateral plates and terminate near the flexure of the great grooves, close behind the origin of its small outer branch.

Stensiö (1931) bases his definition of *Bothriolepis* on the above characteristics. He says; " . . . Oblique pit-line of the head and subrostral pit-line present and well developed . . . " The definition should be expanded to include species without the V-shaped groove of the lateral lines on the median occipital (oblique pit-line), such as *B. stensiöi*, n. sp.

BOTHRIOLEPIS CANADENSIS
Whiteaves, 1880
Text figure 2

Bothriolepis canadensis WHITEAVES, *1880*, Am. Jour. Sci., 3d ser., vol. 20, p. 135.—WHITEAVES, *1887*, Roy. Soc. Canada Trans., sec. 4, pp. 101–107, pl. 6, fig. 1, pl. 8.—EASTMAN, *1907*, New York State Mus. Mem. 10, pp. 43–49, text figs. 10–12.

Many well-preserved specimens of this species, which have contributed a great deal to the knowledge of the genus, have been found. The lateral line system of the cephalic shield is typical of the genus and illustrates the V-shaped groove on the median occipital.

BOTHRIOLEPIS STENSIÖI Sohn, n. sp.
Text figures 1a, b

The specimen upon which this species is based is a well-preserved cephalic shield taken from a sandstone concretion. The plates present are the premedian, postmedian, median occipital, laterals, lateral occipitals, and angulars. The shape and arrangement of the plates is typical of *Bothriolepis*.

This species has a branch of the lateral-line grooves that runs forward and outward to the margin of the shield on the lateral plates (subrostral pit-line), but does not have the V-shaped groove on the median occipital.

The head appears to be more convex than *B. canadensis;* the surface coarsely tuberculated.

This species is named in honor of Dr. E. A. Stensiö, of Stockholm, who contributed much to the knowledge of Placodermata.

Holotype.—Columbia Univ. Paleont. coll. 26041.

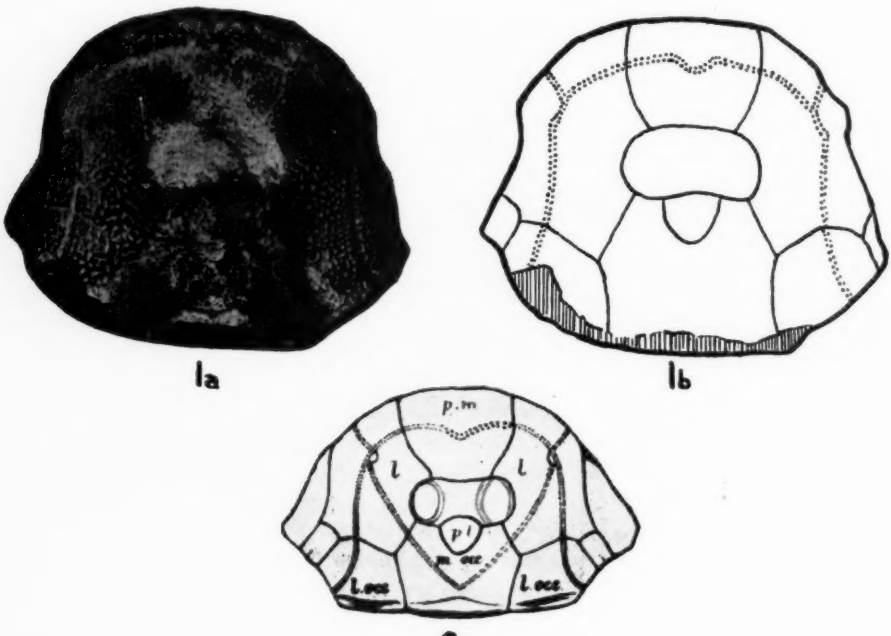

FIG. 1—*Bothriolepis stensiöi* Sohn, n. sp. 1*a*, Holotype, dorsal view, ×1. 1*b*, Sketch showing the arrangement of plates and of the lateral-line groove system.
2—*Bothriolepis canadensis* Whiteaves, from Traquair 1888, showing the arrangement of plates and the lateral-line system.

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PALEONTOLOGICAL NOTE

NOMENCLATURE OF *LINDSTRÖMIA* NICHOLSON AND THOMSON AND ITS GENOTYPE

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During the work on a catalogue of Paleozoic corals it has been interesting but rather disturbing to note the multiplicity of opinions published in regard to the genotypes of certain genera. It has been thought worth while to discuss in a separate note the opinions of several authors in regard to *Lindströmia* and its genotype because these opinions have been at such variance and none of them, insofar as nomenclature is concerned, correct.

The first citation of *Lindströmia* appeared in 1876 in an abstract of a paper by Nicholson and Thomson (1). The abstract reads:

. . . Finally, the genus *Lindströmia* was proposed for a group of small corals, in which the corallum is simple and conical, with an extremely deep calice. The septa are well developed, and meet in the centre of the visceral chamber, where they coalesce to a greater or less extent, and form a long twisted pseudocolumella which projects into the floor of the calice, and occupies a large portion of the visceral chamber. There are no tabulae, but the septa are furnished with more or less strongly developed dissepiments, which, however, are remote, and do not give rise to any visceral zone. The genus may, perhaps, be regarded as belonging to the *Aporosa*. The species, *L. columnaris* was described from the Devonian rocks of North America, and it was mentioned that the authors were in possession of other forms of the genus, still undescribed, from the Carboniferous rocks of Scotland.

It is to be noted that in this abstracted form only a description of the genus is given, with merely the mention of a single species, *L. columnaris*. In 1878, Nicholson and Etheridge, Junior (2), published in their "Monograph of the Silurian Fossils of the Girvan District in Ayrshire" figures of *L. columnaris* Nicholson and Thomson from the Devonian rocks of North America and in 1889 Miller (3) designated this species as genotype of *Lindströmia*. Should there be any doubt as to whether or not *L. columnaris* is to be accepted as the genotype on the basis of the original description of the genus with mere mention of the species, the later designation by Miller settles the question definitely.

Chapman's statement (4) that the authorship of species should go to Nicholson and Etheridge, because with their publication of the figures of *L. columnaris* the "actual structure of the genotype" is known for the first time, is quite beside the point. In the plate description authorship is definitely given to the original authors of the genus, Nicholson and Thomson.

In 1928 Grabau (5) published an opinion that because the Devonian species, *L. columnaris* of Nicholson and Thomson, had never been described, an Ordovician and a Silurian species, *Petraia subduplicata* McCoy and *L. laevis* Nicholson and Etheridge respectively, described by Nicholson and Etheridge in their Girvan Monograph, "really

must be taken as the types of the genus."[1] As stated above, the publishing (in 1878) of figures of *L. columnaris* Nicholson and Thomson validates the species, and Miller's designation (1889) of the species as genotype definitely fixes *L. columnaris* as the genotype of *Lindströmia*. According to the International Rules of Zoological Nomenclature "such designation is not subject to change."

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[1] Grabau omits from those species that he considers "must be taken as the types of the genus" an additional species assigned by Nicholson and Etheridge to *Lindströmia*, namely *Cyathaxonia dalmani* Edwards and Haine. Another species, *Cyathaxonia siluriensis* McCoy, which Nicholson and Etheridge state "is also clearly a *Lindströmia*" is discussed by Butler (6), who selects it as the genotype of *Syringaxon* Lindström, 1882.

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